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Larval development and identification of the genus *Triglops* (Scorpaeniformes: Cottidae)

Deborah M. Blood
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Larval development and identification of the genus *Triglops* (Scorpaeniformes: Cottidae)

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Abstract—Prior to Pietsch's (1993) revision of the genus *Triglops*, identification of their larvae was difficult; six species co-occur in the eastern North Pacific Ocean and Bering Sea and three co-occur in the western North Atlantic Ocean. We examined larvae from collections of the Alaska Fisheries Science Center and Atlantic Reference Centre and used updated meristic data, pigment patterns, and morphological characters to identify larvae of *Triglops forficatus*, *T. macellus*, *T. murrayi*, *T. nybelini*, *T. pingeli*, and *T. scepticus*; larvae of *T. metopias*, *T. dorothy*, *T. jordani*, and *T. xenostethus* have yet to be identified and are thus not included in this paper. Larval *Triglops* are characterized by a high myomere count (42–54), heavy dorsolateral pigmentation on the gut, and a pointed snout. Among species co-occurring in the eastern North Pacific Ocean, *T. forficatus*, *T. macellus*, and *T. pingeli* larvae are distinguished from each other by meristic counts and presence or absence of a series of postanal ventral melanophores. *Triglops scepticus* is differentiated from other eastern North Pacific Ocean larvae by having 0–3 postanal ventral melanophores, a large eye, and a large body depth. Among species co-occurring in the western North Atlantic Ocean, *T. murrayi* and *T. pingeli* larvae are distinguished from each other by meristic counts (vertebrae, dorsal-fin rays, and anal-fin rays once formed), number of postanal ventral melanophores, and first appearance and size of head spines. *Triglops nybelini* is distinguished from *T. murrayi* and *T. pingeli* by a large eye, pigment on the lateral line and dorsal midline in flexion larvae, and a greater number of dorsal-fin rays and pectoral-fin rays once formed.

Introduction

Sculpins of the family Cottidae are important components of North Pacific Ocean ecosystems. Nearly 200 species are found in the North Pacific Ocean in almost every benthic marine habitat from the intertidal to the upper continental slope (Pietsch and Orr, 2006). Despite such diversity and abundance, the systematics and life histories, especially of their early stages, are poorly known. Recent genetic studies on the higher level relationships of the family Cottidae have demonstrated the urgent need for more comprehensive morphological studies including ontogenetic characters (Smith and Wheeler, 2004).

The genus *Triglops* is recognized as having 10 species worldwide (Table 1; Pietsch, 1993; Pietsch and Orr, 2006). Although morphologically distinct, the phylogenetic relationships of this genus to other cottid taxa have not been fully resolved. Species of *Triglops* are characterized in part by having a small head, a narrow, elongate body, slender caudal peduncle, long anal fin containing 18–32 fin rays, and scales below the lateral line modified to form discrete rows of small, serrated plates that lie in close-set, oblique dermal folds. Adults are generally distributed in shallow to moderately deep water (18–600 m) throughout the coldwater continental shelf or slope regions of the North Pacific, North Atlantic, and Arctic oceans.

Prior to Pietsch (1993), the genus was in need of revision. Identification of the larvae was possible usually only to the level of genus owing to a vertebral range (42–54) that is higher than in most cottids. Because much of the meristic data for individual species were unavailable, specific identification of the larvae was difficult. Species of *Triglops* for which larvae were previously described include *T. pingeli*, *T. murrayi*, and *T. nybelini*, all of which occur in the North Atlantic Ocean; however, descriptions published for *T. pingeli* were incomplete or based on misidentified specimens, and the description of *T. nybelini* was incomplete. Ehrenbaum (1905–1909), Dunbar (1947), and Rass (1949) each described and illustrated one specimen of *Triglops pingeli* (18 mm, 28 mm, and 10 mm, respectively). Koefoed (1907) described a series of eight larvae as *Triglops pingeli* (10–22 mm); dorsal-fin ray counts of five of these larvae indicate that they probably were misidentified specimens of *T. murrayi*. Larvae of *Triglops murrayi* (8.4–23.4 mm) have been described by Khan (1972) and Fahay (1983, 2007); Pavlov et al. (1992) described both eggs and larvae (8.0–20.2 mm) of this species. Dunbar and Hildebrand (1952) presented a description and photograph of a 27-mm SL larva of *Triglops nybelini*. Two larvae from Puget Sound, Washington, identified as *Triglops* sp. were illustrated by Blackburn (1973); Richardson and Washington (1980)

Table 1

Meristic characters and distribution of the genus *Triglops* (Pietsch, 1993; Pietsch and Orr, 2006; Mecklenburg et al., 2002). Pelvic-fin ray counts are I, 3 for all species.

Taxon	Distribution	Vertebrae	Fin elements		
			Dorsal	Anal	Pectoral
Triglops dorothy	Southern Sea of Okhotsk	45–47	X–XI, 23–25	23–25	17–19
Triglops forficatus	Bering Sea, Gulf of Alaska, North Pacific Ocean to Cook Inlet, AK	52–54	X–XI, 28–30	29–32	20–22
Triglops jordani[1]	Japan and Okhotsk seas, western Bering Sea	47–49	IX–XI, 25–29	26–29	18–21
Triglops macellus	Aleutian Is. and eastern Bering Sea, Gulf of Alaska to Washington	49–51	X–XII, 28–31	27–31	15–17
Triglops metopias	Aleutian Is. and Gulf of Alaska to Auke Bay, AK	47–49	X–XI, 24–28	24–28	19–22
Triglops murrayi	North Atlantic and Arctic Oceans	42–47	X–XII, 19[2]–24	18–23	16–20
Triglops nybelini	North Atlantic and Arctic Oceans	46–49	X[3]–XII, 24–29	24–28	20–23
Triglops pingeli	North Atlantic and Arctic Oceans, North Pacific Ocean to Puget Sound, WA	45–51	X–XIII, 23–26	21–27	17[4]–21
Triglops scepticus	Japan and Bering seas, Gulf of Alaska to Southeast Alaska	45–46	X–XII, 21–24	22–25	18–20
Triglops xenostethus[5]	Kuril and Commander Is., southern Bering Sea and Aleutian Is.	43–46	X–XI, 22–24	22–24	15–18

[1] According to Mecklenburg et al. (2002), specimens of *T. jordani* were reported near the Pribilof Islands, but records are not verified and no voucher specimen is available.

[2] According to Andriashev (1949), the minimum number of dorsal-fin rays for *T. murrayi* is 18.

[3] According to Andriashev (1949), the minimum number of dorsal-fin spines for *T. nybelini* is IX.

[4] According to Andriashev (1949), the minimum number of pectoral-fin rays for *T. pingeli* is 16.

[5] According to Mecklenburg et al. (2002), a single *T. xenostethus* was reported from the Pribilof Islands, but no voucher specimen is available.

described similar larvae collected in the eastern North Pacific Ocean, but were unable to identify them to species. Matarese et al. (1989) presented illustrations of *Triglops* A and *Triglops* B larvae (*Triglops* sp. in Richardson and Washington [1980]) and provided general characters that enabled identification. Based on the few meristic counts available at the time, they suggested that *Triglops* A could be *T. scepticus*.

Updated distributional and meristic information in Pietsch (1993) and Pietsch and Orr (2006) provides enough information to identify larvae from the eastern North Pacific Ocean and add to the body of knowledge about those larvae previously identified. Specific distributional records cited in Mecklenburg et al. (2002) also have helped clarify the problem by narrowing what species are likely to spawn in the eastern North Pacific Ocean. In this paper, we describe and illustrate the first complete series of larvae of *Triglops forficatus*, *T. macellus*, and *T. scepticus*; preflexion and flexion larvae are described and illustrated for *T. nybelini*, completing historical developmental series. We present a revised series and description of larvae of *Triglops pingeli* and *T. murrayi*, and describe characters which differentiate these two species in the western North Atlantic Ocean where they co-occur. Larvae of *T. dorothy* (Sea of Okhotsk), *T. jordani* (Japan and Okhotsk seas), *T. metopias* (Aleutian Islands and Gulf of Alaska), and *T. xenostethus* (Kuril, Commander, and Aleutian Islands) remain undescribed.

Methods and materials

Many of the larvae examined for this study were collected in Puget Sound, Washington; the northern Gulf of Alaska; and the Bering Sea. Ichthyoplankton data were obtained from surveys conducted by the Alaska Fisheries Science Center (AFSC) Recruitment Processes Program. Collection data for cruises prior to 1988 were found in Dunn and Rugen (1989[1]), and those from 1989 to 2005 in the AFSC ichthyoplankton cruise database (Rugen, 2000[2]). The University of Washington Fish Collection (UW) was another source

[1] Dunn, J. R., and W. C. Rugen. 1989. A catalog of Northwest and Alaska Fisheries Center ichthyoplankton cruises 1965–1988. AFSC Proc. Rep. 89-04, 87 p. AFSC, NMFS, NOAA, 7600 Sand Point Way NE, Seattle, WA 98115.

[2] Rugen, W. C. 2000. Alaska Fisheries Science Center Ichthyoplankton Cruise Database. Resource Assessment and Conservation Engineering Division, 7600 Sand Point Way NE, Seattle, WA 98115. http://access.afsc.noaa.gov/icc/openframe.cfm. [Accessed: October 2009.]

of specimens, including material provided by the Vancouver Public Aquarium. Most larvae were collected using 60-cm bongo nets and originally fixed in 5% buffered formalin. Larvae were later transferred to and stored in 70% ethanol. A detailed account of sampling and identification protocols is available in Matarese et al. (2003).

Additional material, collected from the Bay of Fundy, Gulf of Maine, and western North Atlantic Ocean off Nova Scotia and Newfoundland, was obtained from the Atlantic Reference Centre (ARC) of the Huntsman Marine Science Centre in New Brunswick, Canada. The collection gear listed for some of these larvae is sawtooth bongo (Stephenson and Power, 1988), which is a bongo net that is towed in stepped intervals instead of the standard MARMAP (Marine Resources Monitoring, Assessment, and Prediction) oblique sampling procedure (Smith and Richardson, 1977).

Larvae were identified using the serial approach. This method uses adult characters to identify juveniles and progressively links them to smaller specimens through a continuous sequence of shared or similar features. For this study, characters of *Triglops* species described by Pietsch (1993), especially meristic counts, were used to progressively link juveniles to smaller specimens. Developmental series were illustrated using a camera lucida attached to a dissecting microscope. Only dark melanistic pigment is described because formalin fails to preserve other color pigments. The best representative specimen of each taxon at each stage of development (preflexion, flexion, and postflexion) was illustrated. Whereas pigmentation among specimens was variable, some pigment described in the taxon accounts may not be visible on the illustrations. Descriptions and illustrations of anatomical and morphometric features and other terms used herein to describe placement of pigment can be found in Matarese et al. (1989) and Moser (1996).

Measurements, taken on the left side of the fish when possible, were made using a calibrated digital image analysis system. The system consists of a video camera attached to a dissecting stereomicroscope or camera lens, a computer with a digital imaging board, and a video monitor. Only larvae that were not badly damaged during collection or preservation were measured. The following measurements were made on larvae:

Standard length (SL): Snout tip to notochord tip prior to development of caudal fin (defined as principal caudal-fin rays formed); to posterior margin of hypural element in flexion and postflexion larvae. All body lengths in this study are standard lengths.

Snout to anus length: Distance along body midline from snout tip to a vertical line drawn through center of anal opening.

Snout to first dorsal-fin length: Distance along body midline from snout tip to a vertical line drawn at the origin of the first dorsal-fin ray.

Body depth: Vertical distance from dorsal to ventral body margin at the anus.

Head length (HL): Snout tip to posterior edge of opercle bone.

Snout length: Snout tip to anterior margin of orbit of left eye.

Eye diameter: Greatest distance across the left orbit. This measurement can be taken horizontally, vertically, or diagonally.

Interorbital width: Distance across head between dorsal margins of orbit.

Pectoral-fin ray length: Length of longest fin ray of pectoral fin, from distal edge of pectoral-fin base to tip of fin ray.

Measurements of morphological features listed above are reported as mean percent of SL or HL except for standard length. Using the morphometric measurements, an analysis of covariance (ANCOVA) was performed to determine whether there were any significant differences among species at preflexion, flexion, or postflexion stages when all species were combined as well as within two species groups. These groups were composed of those species co-occurring in the eastern North Pacific Ocean and Bering Sea (Pacific species: *Triglops forficatus*, *T. macellus*, *T. pingeli*, and *T. scepticus*) and the western North Atlantic Ocean (Atlantic species: *T. murrayi*, *T. nybelini*, and *T. pingeli*). If the test for species*covariate (SL or HL) interaction (the first step of the ANCOVA) was not significant, the second step was to test whether SL or HL was significant. If not significant, the covariate was dropped from the model and the slope of the final plotted "trendline" was equal to zero; otherwise, the covariate remained in the model to test for species. When the overall ANCOVA test for species was significant ($P<0.05$), pairwise comparisons were run. In comparisons between two species affected by low sample size, the ANCOVA/ANOVA was followed by pairwise tests with a Tukey-Kramer adjustment to investigate if any trends had been overlooked (Sokal and Rohlf, 1995).

When sufficient numbers of specimens were available, selected specimens were cleared and differentially stained to count meristic structures (Pothoff, 1984). Skeletal elements were recognized as ossified upon initial uptake of alizarin red-S. Larval head spines were examined; head spine terminology follows Richardson and Laroche (1979).

Distribution maps were made using data from the AFSC ichthyoplankton database or from additional larvae obtained from other collections. Sample size of

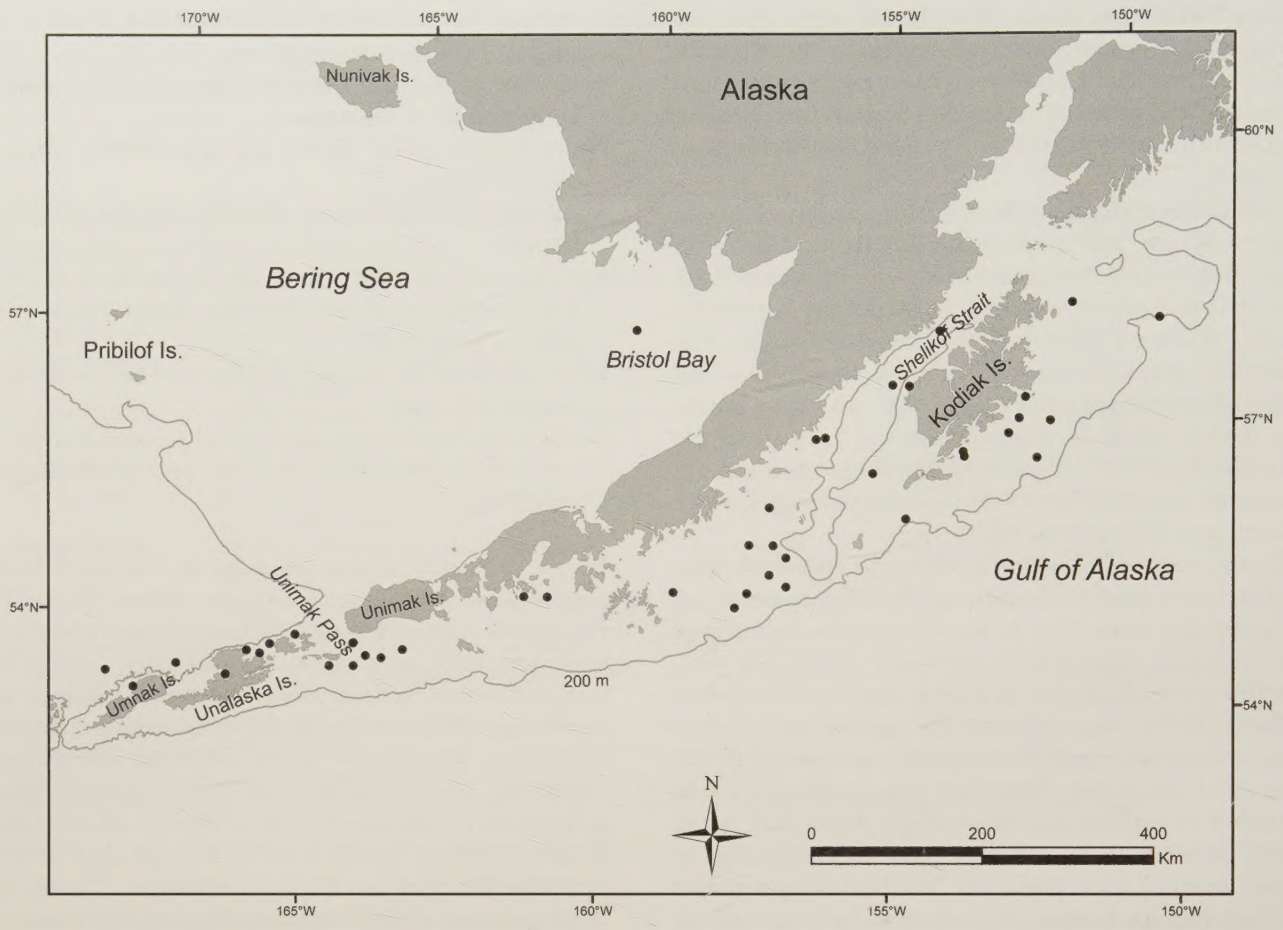

Figure 1

Distribution of all known records, including material examined here, of larvae of *Triglops forficatus* in the Bering Sea and Gulf of Alaska. Each symbol may indicate more than one capture; bathymetry line equals 200 m.

some taxa was limited and may not reflect their entire distributional range, especially in the western North Atlantic Ocean.

Identification of genus

Larvae of the genus *Triglops* are distinguished from other cottid genera by the following combination of characters: moderately slender body shape, obliquely placed mouth, angular jaw, pointed snout, and a high vertebral count, usually ≥45 (*T. murrayi* = 42–47). In addition, after fin and scale development, *Triglops* juveniles and adults may be identified by the following characters: a long anal fin, scales below lateral line modified to form discrete rows of tiny serrated plates that lie in close-set, oblique dermal rows, slender caudal peduncle, and a small head with a narrow elongate body (Pietsch and Orr, 2006).

Species accounts

Triglops forficatus, scissortail sculpin (Figs. 1–2)

Material examined. 28 specimens (7.7–28.0 mm SL) examined. Bering Sea: UW 126002, 3 (12.0–19.1 mm), 54°0.30′N, 166°21.0′W, 0–81 m depth, Tucker net, 02 June 1986; UW 125832, 1 (15.9 mm), 53°43.0′N, 166°53.0′W, 0–105 m depth, Tucker net, 04 June 1986; UW 125833, 1 (15.9 mm), 54°16.0′N, 165°47.0′W, 0–46 m depth, Tucker net, 05 June 1986; UW 125834, 1 (8.0 mm), 53°23.4′N, 168°26.4′W, 0–44 m depth, bongo net, 20 April 1993; UW 125836, 1 (9.8 mm), 57°55.3′N, 160°07.9′W, 0–35 m depth, bongo net, 22 May 1976; UW 125837, 1 (8.1 mm), 53°30.0′N, 169°58.9′W, 0–530 m depth, bongo net, 11 March 1991. Gulf of Alaska: UW 035569, 1 (9.0 mm), 56°59.0′N, 152°47.0′W, 0–127 m depth, bongo net, 16 April 1987; UW 035858, 2 (7.8–9.6 mm), 54°0.0′N, 165°05.0′W, 0–74 m depth,

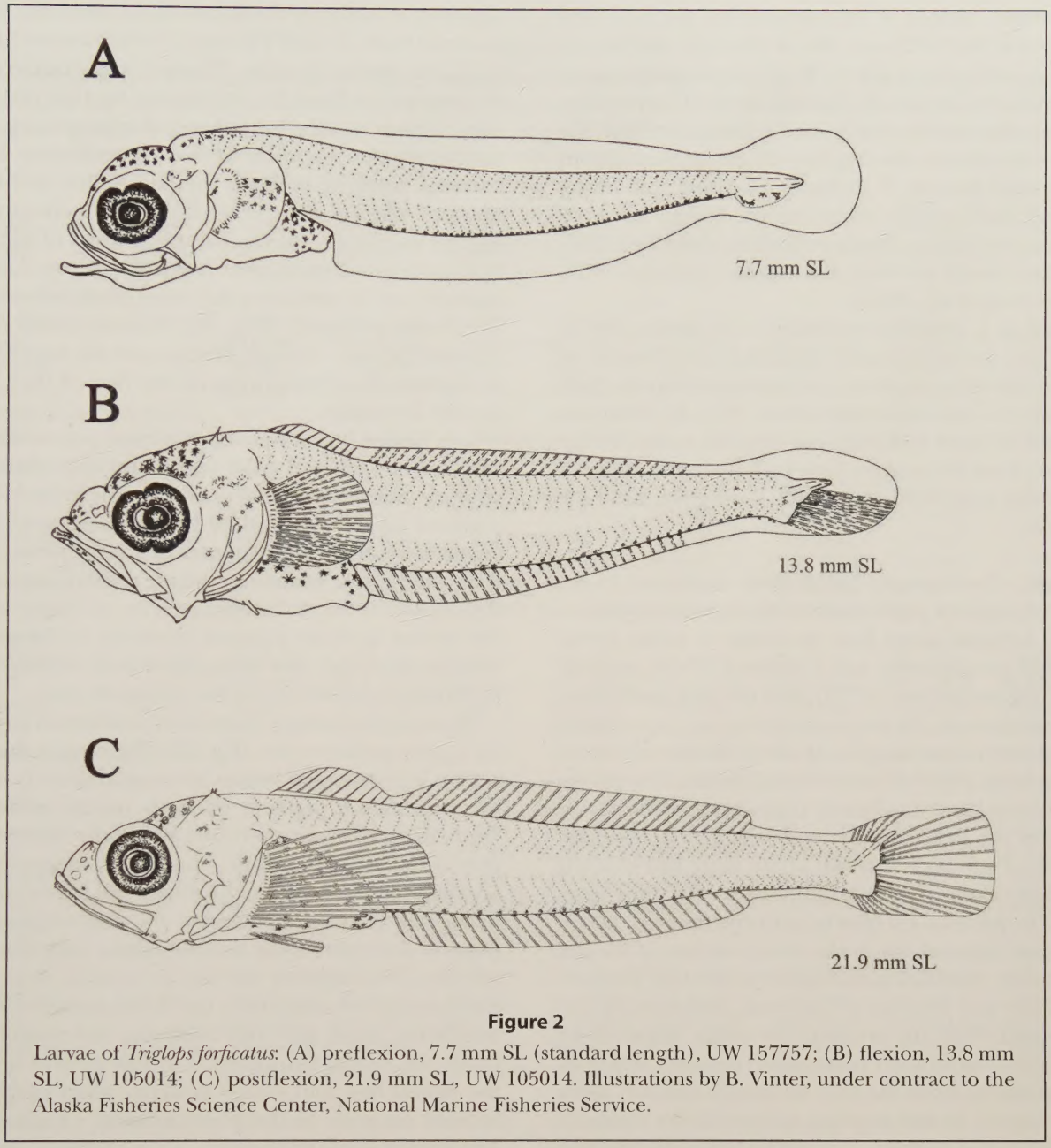

Figure 2

Larvae of *Triglops forficatus*: (A) preflexion, 7.7 mm SL (standard length), UW 157757; (B) flexion, 13.8 mm SL, UW 105014; (C) postflexion, 21.9 mm SL, UW 105014. Illustrations by B. Vinter, under contract to the Alaska Fisheries Science Center, National Marine Fisheries Service.

bongo net, 27 April 1987; UW 039511, 1 (10.8 mm), 55°20.0′N, 156°57.0′W, 0–81 m depth, bongo net, 14 April 1986; UW 039930, 1 (9.6 mm), 57°21.5′N, 152°26.5′W, 0–48 m depth, bongo net, 15 February 1979; UW 105014, 3 (13.8–21.9 mm), 58°20.0′N, 151°28.0′W, 0–74 m depth, Tucker net, 25 May 1986; UW 125838, 1 (19.6 mm), 56°55.0′N, 156°19.0′W, 0–159 m depth, Tucker net, 29 May 1986; UW 056815, 1 (9.2 mm), 58°07.5′N, 149°45.0′W, 0–197 m depth, bongo net, 07 March 1981; UW 157757, 1 (7.7 mm), 56°05.0′N, 154°45.0′W, 0–34 m depth, bongo net, 24 April 1984; UW 125841, 1 (10.4 mm), 56°43.0′N, 152°15.0′W, 0–60 m depth, bongo net, 01 May 1972; UW 062274, 1 (11.6 mm), 58°03.4′N, 154°06.8′W, 0–104 m depth, bongo net, 08 May 1990; UW 068070, 2 (9.2–10.3 mm), 56°53.9′N, 156°29.5′W, 0–87 m depth, bongo net, 13 May 1989; UW 125842, 1 (14.6 mm), 57°28.7′N, 154°42.3′W, 0–56 m depth, bongo net, 01 May 1991; UW 069224, 1 (9.2 mm), 56°43.9′N, 153°39.6′W, 0–68 m depth, Tucker net, 10 April 1978; UW 125843, 1 (9.6 mm), 56°44.6′N, 153°38.3′W, 0–132 m depth, Tucker net, 10 April 1978; UW 069932, 1 (9.2 mm), 57°08.3′N, 152°34.5′W, 0–109 m depth, Tucker net, 08 April 1978; UW 071583, 1 (11.7 mm), 55°38.4′N, 156°58.5′W, 0–78 m depth, bongo net, 30 May 1990.

Occurrence. Adults of *Triglops forficatus* are restricted to the North Pacific Ocean, Sea of Okhotsk, and Bering Sea. They are found from the Kuril Islands and western Kamchatka in the Sea of Okhotsk to the Commander Islands in the western North Pacific Ocean, to Cape Navarin in the western Bering Sea. Reported throughout the Aleutian Islands, *T. forficatus* are also found along the outer shelf regions of the eastern Bering Sea, eastward into the Gulf of Alaska to Kodiak Island and Cook Inlet, and south to Southeast Alaska (Pietsch, 1993; Mecklenburg et al., 2002).

Larvae of *T. forficatus* are found in the Bering Sea in Bristol Bay, around Umnak, Unalaska, and Unimak Islands in the Aleutian chain, and eastward into the Gulf of Alaska to east of Kodiak Island (Fig. 1). Most are collected in April and May, but they are found in the plankton from February to June inshore in the Aleutian Islands and over shelf areas in the Bering Sea and Gulf of Alaska.

Pigment. Twenty-eight larvae were examined to describe changes in pigmentation during development. *Triglops forficatus* larvae have moderate to heavy dorsal head and gut pigment, and a series of 21–53 postanal ventral melanophores (PVM) that become embedded with development. In some specimens, an interrupted series of internal melanophores above the lateral line extending from midbody to the caudal peduncle is visible.

Preflexion larvae are heavily pigmented on the dorsal surface of the head from between the eyes to the nape (Fig. 2A). Pigment is internal at the nape and extends posteriorly along the dorsal midline to the third myomere. The pectoral-fin base is lightly pigmented. Heavy peritoneal pigment covers the dorsal surface of the gut and smaller external melanophores encircle the portion of the gut anterior to the anus. Between 24 and 53 internal PVM are present; the series begins 6–12 (usually 6–7) myomeres posterior to the anus and ends 1–4 myomeres from the tail. Melanophores are more widely spaced in the anterior section of the series. A line of internal pigment located on the posterior half of the body near the dorsal margin is visible in some specimens; number (5–17) and spacing of this series is highly variable. Several melanophores are visible on the hypural anlage and are variable in number (2–5).

With development (8–9 mm SL), pigment can be seen under the gill cover. Internal pigment develops in the otic area and on the lateral surface of the gut. In some specimens, internal pigment also appears on the ventral surface of the gut. Pigment is visible on the ventral caudal finfold; there may be up to 10 melanophores in the ventral caudal fin area (finfold and hypural anlagen).

Early flexion stage larvae (about 10–11 mm SL) develop pigment on the lower jaw and on the anterior portion of the median cartilage between the dentaries. Fine pigment is visible on the dorsal rim of the orbit. On the postanal body, 21–52 PVM begin 3–8 myomeres (usually 5–7) posterior to the anus. This series extends to within 3–4 myomeres from the developing hypural plate or it may extend onto the lower hypural area; spacing of the melanophores is similar to that in preflexion larvae. Internal pigment between the lateral line and dorsal margin, when visible, consists of 8–9 melanophores spaced irregularly on the posterior third of the body and ending 2–3 myomeres from the tail tip. External pigment can be seen near the notochord in the area of the caudal peduncle (Fig. 2B). Ventral caudal finfold pigment persists through flexion and the number and placement of melanophores on the base of the caudal-fin rays is variable.

Late flexion larvae develop increased pigment on the snout, lower jaw, and gular region. Internal pigment is visible in the preopercular area posterior to the eye, and pigment on the pectoral-fin base is more prominent. Postanal ventral melanophores begin to move inward from the ventral midline in the area where the anal fin develops to form an incomplete row on either side of the ventral midline; pigment posterior to the anal fin remains in a single row along the ventral midline. A few melanophores develop on the caudal-fin base.

Pigment continues to increase in postflexion larvae on the upper and lower jaw (Fig. 2C). Pigment in the gular region increases and begins to move anteriorly toward the chin. Snout pigment becomes mostly embedded. Pigment on the gut now covers all but the anterior portion of the ventral midline, and ventral melanophores are smaller than those on the dorsal and lateral surfaces of the gut. On some specimens, two melanophores appear on each side of the dorsal midline near dorsal-fin soft rays 7–8. Pigment can also be seen in some specimens along and adjacent to the dorsal midline over the hindbrain, nape, gut, and midbody, and scattered towards the caudal fin. Internal melanophores between the lateral line and dorsal midline, when visible, are located on each of the posteriormost 13 myomeres. The postanal ventral pigment series has 26–33 melanophores that begin 1–10 myomeres posterior to the anus and continue as an incomplete row on either side of the ventral midline to the end of the anal fin. Pigment on the caudal-fin base is mostly internal and restricted to the lower hypural area. Upper and lower principal caudal-fin rays each have 3–4 melanophores at the base.

Proportions. Notochord flexion in *Triglops forficatus* begins about 9 mm SL; most larvae have completed flexion by 17 mm SL. Most body measurements increase throughout development (Table 2). Snout length/HL increases less than any body part measured, pectoral-fin length/SL increases more than any body part measured, and eye diameter/HL decreases throughout development.

Table 2

Proportional measurements for larvae of *Triglops forficatus, T. macellus, T. murrayi, T. nybelini, T. pingeli,* and *T. scepticus.* Proportions are expressed as percent of standard length (SL) except for snout length, eye diameter, and interorbital width, which are expressed as percent of head length (HL). Values are mean, standard deviation, and range (in parentheses).

Species Stage	Standard length (mm)	Length to anus length/SL	Snout to first dorsal-fin length/SL	Body depth/SL	Head length/SL	Snout length/HL	Eye diameter/HL	Interorbital width/HL	Pectoral-fin length/SL
Triglops forficatus									
Preflexion	7.7–10.4	36.3±1.8	22.9±2.1	9.4±0.9	21.0±2.0	24.7±5.2	45.4±5.7	26.4±4.8	7.0±1.3
n=11		(33.3–39.2)	(20.1–27.7)	(7.8–10.4)	(18.1–24.7)	(15.0–35.9)	(36.6–53.6)	(18.0–34.5)	(3.9–9.1)
Flexion	9.2–16.7	40.0±2.5	26.4±2.5	11.3±1.6	24.5±3.0	26.8±5.3	38.3±5.9	23.1±3.3	9.6±2.9
n=12		(36.8–43.9)	(22.2–31.1)	(9.3–13.7)	(20.2–29.1)	(16.9–33.4)	(30.0–47.3)	(18.4–29.1)	(6.1–14.8)
Postflexion	15.9–21.9	42.2±1.9	28.8±1.4	13.3±0.5	27.2±2.3	27.3±2.7	32.4±2.6	25.7±3.2	18.8±1.1
n=5		(40.2–44.9)	(27.0–30.6)	(12.9–14.2)	(24.7–30.5)	(23.3–31.1)	(28.2–34.3)	(22.5–30.2)	(17.2–20.1)
T. macellus									
Preflexion	7.3–9.6	36.7±2.4	23.4±1.2	8.5±1.0	20.5±1.5	16.4±4.6	46.0±3.7	28.9±4.8	6.6±1.1
n=8		(33.7–41.1)	(21.8–25.0)	(7.2–9.6)	(18.3–22.9)	(12.1–25.1)	(40.1–50.8)	(23.3–37.1)	(4.7–8.0)
Flexion	9.4–14.8	44.6±2.5	28.7±2.1	13.7±2.0	27.0±3.6	26.2±3.5	37.0±5.0	26.9±4.2	12.7±4.2
n=17		(40.4–49.7)	(24.2–31.6)	(10.2–17.2)	(20.8–32.2)	(18.8–31.3)	(29.5–44.8)	(21.0–34.5)	(5.7–21.5)
Postflexion	17.2–20.3	43.6±1.4	28.3±2.1	14.5±0.8	28.3±2.2	28.7±2.6	33.2±4.5	23.7±2.7	21.2±2.0
n=7		(42.1–46.2)	(24.7–31.0)	(13.7–15.4)	(25.4–31.9)	(24.7–32.0)	(27.7–40.5)	(20.3–28.2)	(17.8–23.0)
T. murrayi									
Preflexion	9.2–10.3	38.4±1.2	25.2±2.4	10.7±0.4	22.1±0.7	29.6±3.3	37.9±1.4	24.7±3.0	5.5±0.9
n=3		(37.2–39.7)	(23.1–27.8)	(10.3–11.1)	(21.5–22.8)	(26.2–32.8)	(36.5–39.3)	(21.4–27.2)	(4.8–6.5)
Flexion	10.5–17.5	45.4±2.3	28.1±1.6	12.4±0.8	25.6±2.1	32.6±2.9	30.8±4.1	23.6±3.7[1]	10.4±3.8
n=12		(41.2–49.8)	(24.8–30.9)	(11.1–13.5)	(21.4–28.4)	(24.6–37.7)	(26.5–40.6)	(19.2–32.0)	(5.7–19.1)
Postflexion	18.7–23.4	44.1±2.2	26.7±2.1	12.7±2.2	27.1±3.2	31.4±4.2	26.8±2.1	19.9±2.5	21.3±3.5[2]
n=4		(41.0–45.8)	(24.0–29.1)	(10.9–15.4)	(22.4–29.8)	(25.9–35.9)	(24.8–29.6)	(16.6–22.2)	(18.3–25.1)
T. nybelini									
Preflexion	8.0–10.1	36.3±1.1	22.4±0.6	9.1±0.8	20.4±1.1	23.2±7.2	47.3±2.7	35.3±1.1	6.3±1.0
n=3		(35.1–37.0)	(22.0–23.0)	(8.2–9.6)	(19.1–21.2)	(17.0–31.0)	(44.2–49.3)	(34.1–36.3)	(5.3–7.4)
Flexion	11.5–14.4	44.9±1.6	31.3±2.6	13.1±3.0	25.4±0.1	27.0±1.8	36.9±2.5	28[3]	9.9±3.9
n=2		(43.8–46.0)	(29.5–33.1)	(11.0–15.2)	(25.3–25.4)	(25.7–28.3)	(35.2–38.7)		(7.1–12.7)
T. pingeli									
Preflexion	6.2–10.1	36.3±2.9	22.3±2.6	9.1±1.2	21.2±2.7	23.5±5.4	43.5±5.3	32.5±8.2	6.7±1.4
n=16		(32.4–42.5)	(19.7–27.8)	(7.0–10.9)	(17.7–28.1)	(13.4–31.6)	(33.1–51.5)	(19.7–48.3)	(3.7–8.9)
Flexion	9.8–14.3	43.9±2.4	28.2±2.4	12.3±1.3	26.4±3.7	31.1±4.3	32.6±5.0	25.4±4.3	10.1±3.0
n=15		(40.3–48.1)	(23.4–34.3)	(10.2–15.5)	(20.7–32.5)	(22.3–37.9)	(24.9–40.0)	(18.9–34.1)	(4.7–17.6)
Postflexion	15.3–18.1	45.5±1.8	29.3±2.0	14.7±0.7	30.9±2.0	30.4±2.7	27.0±1.9	20.8±4.2	20.4±1.8
n=6		(42.2–47.6)	(27.6–33.1)	(13.6–15.4)	(28.2–34.3)	(28.2–34.1)	(24.4–29.3)	(13.2–25.2)	(17.7–22.4)
T. scepticus									
Preflexion	9.0–9.3	39.7±4.4	24.4±1.5	10.7±2.0	23.5±0.4	25.8±4.2	46.4±4.2	29.0±3.4	7.1±0.6
n=2		(36.6–42.8)	(23.4–25.4)	(9.3–12.1)	(23.3–23.8)	(22.8–28.7)	(43.4–49.4)	(26.5–31.4)	(6.6–7.5)
Flexion	13.6–16.7	48.9±1.6	29.9±2.1	17.5±0.7	30.4±1.3	27.2±2.6	36.9±1.4	28.8±2.3	14.2±3.4
n=4		(47.5–51.2)	(28.5–33.0)	(16.7–18.3)	(29.1–32.0)	(23.8–30.3)	(35.4–38.6)	(26.5–31.8)	(9.2–16.6)
Postflexion	18.5–19.0	47.9±3.7	28.8±0.9	17.2±2.2	30.1±1.0	26.4±5.9	33.1±1.8	37.2±12.9	21.0±5.7
n=2		(45.3–50.4)	(28.2–29.5)	(15.7–18.8)	(29.4–30.8)	(22.2–30.5)	(31.8–34.3)	(28.1–46.3)	(17.0–25.0)

[1] 11 larvae measured.
[2] 3 larvae measured.
[3] 1 larva measured.

Interorbital width/HL decreases from preflexion larvae to flexion larvae, then increases in postflexion larvae.

Spination. Of the specimens available for clearing and staining, no spines are ossified until late flexion (14.6 mm SL). Single parietal, nuchal, postocular, and posttemporal spines are present. A single row of four equal-sized preopercular spines lies posterior to an incomplete anterior row of three spines. The fourth anterior preopercular spine is ossified and the parietal and

Table 3

Summary of meristic and pigment characters useful to distinguish among known *Triglops* larvae. N/A=character not applicable, — = no specimens at a particular stage of development. Values in parentheses = mean±standard deviation and sample size.

	T. forficatus	*T. macellus*	*T. murrayi*	*T. nybelini*	*T. pingeli*	*T. scepticus*
Vertebrae	52–54	49–51	42–47	46–49	45–51	45–46
Dorsal-fin elements	X–XI, 28–30	X–XII, 28–31	X–XII, 19–24	X–XII, 24–29	X–XIII, 23–26	X–XII, 21–24
Anal-fin rays	29–32	27–31	18–23	24–28	21–27	22–25
Pectoral-fin rays	20–22	15–17	16–20	20–23	17–21	18–20
Number of postanal ventral melanophores (PVM)						
preflexion	24–53 (42±10.0, 9)	none	19–26 (23±3.8, 3)	22–45 (35±11.8, 3)	30–49 (37±4.9, 12)	2–3 (2.5±0.7, 2)
flexion	21–52 (35±10.1, 12)	none	11–25 (20±3.6, 11)	20–30 (25±7.1, 2)	23–38 (32±6.4, 10)	2 (2±0, 4)
postflexion	26–33 (30±3.4, 5)	none	21 (21±0, 3)	—	23–34 (27±4.8, 4)	none
Beginning of PVM series (number of myomeres after anus)						
preflexion	6–12	N/A	6–11	6–10	6–10	24
flexion	3–8	N/A	6–14	4	4–9	20
postflexion	1–10	N/A	5	—	5–9	N/A
Ventrolateral pigment						
preflexion	no	no	no	yes	sometimes	yes
flexion	no	no	sometimes	yes	yes	yes
postflexion	no	no	no	—	yes	no
Ventral caudal-fin pigment (number of melanophores)						
preflexion	2–10	no	0–1	0–1	0–1	5–6
flexion	number variable	no	number variable	no	number variable	2
postflexion	3–4	no	3–4	—	0–several	no
Dorsal midline pigment						
preflexion	no	no	no	no	no	no
flexion	no	no	no	yes	no	no
postflexion	sometimes	no	yes (light)	—	no	yes
Dorsolateral pigment						
preflexion	sometimes	no	no	no	no	no
flexion	sometimes; 8–9	no	sometimes	no	no	no
postflexion	sometimes; 13	no	yes (light)	—	no	yes
Dorsal notochord pigment						
preflexion	no	no	no	yes	no	no
flexion	no	no	no	yes	no	no
postflexion	no	no	no	—	no	no

nuchal spines are fused at the base by 18.5 mm SL. The supracleithral and an additional posttemporal spine are ossified by postflexion (20.9 mm SL). Nasal spines are ossified by 23.0 mm SL.

Morphological and other character comparisons. *Triglops forficatus* have the highest number of vertebrae of all *Triglops* species (52–54), a high number of dorsal-fin rays (28–30), the highest number of anal-fin rays (29–32), and a high number of pectoral-fin rays (20–22) (Table 1). Larvae have moderate to heavy head and gut pigment, a ventral midline pigment series with more PVM than other preflexion and flexion stage *Triglops* larvae (up to 53), and the most melanophores in the ventral caudal-fin area (up to 10) (Table 3).

Significant differences in morphological characters between *Triglops forficatus* and all other *Triglops* species are found in flexion stage larvae (Table 4). Larvae of *Triglops forficatus* have a significantly shorter snout to anus length/SL than all other larvae (Appendix 1) and significantly shorter snout to first dorsal-fin length/SL than all except larvae of *T. murrayi* (Table 4). Among those species co-occurring in the eastern North Pacific Ocean and Bering Sea (Pacific species—*Triglops forficatus, T. macellus, T. pingeli,* and *T. scepticus*), larvae of *T. forficatus* have a significantly shorter snout to anus length/SL (Appendix 1; although this is the graph showing all species of *Triglops*, the graph for the western species was identical in relation to the positions of points and equation lines), shorter snout to first dorsal-fin length/SL

Table 4

Summary of morphological characters useful to distinguish among all known larvae of *Triglops*, among known species co-occurring off western North America (Pacific species), and among known species co-occurring off eastern North America (Atlantic species). Entries denote if a species has a statistically significant ($P \leq 0.05$) greater or smaller value than other species. If a species name appears next to an entry, there is no significant difference between it and the taxon name at the top of the column. SL=standard length, HL=head length.

	T. forficatus	*T. macellus*	*T. murrayi*	*T. nybelini*	*T. pingeli*	*T. scepticus*
All species						
Sount to anus length/SL						
preflexion						
flexion	shortest					greatest
postflexion						greatest (*T. murrayi*)
Snout to first dorsal-fin length/SL						
preflexion						
flexion	shortest (*T. murrayi*)					
postflexion						
Body depth/SL						
preflexion						
flexion						greatest
postflexion						greatest (*T. macellus*)
Snout length/HL						
preflexion		shortest (*T. scepticus**)				
flexion			greatest (*T. pingeli*)			
postflexion						
Eye diameter/HL						
preflexion					smallest (*T. murrayi*)	greatest (*T. nybelini*)
flexion					smallest (*T. murrayi*)	greatest
postflexion					smallest (*T. murrayi*)	
Interorbital width/HL						
preflexion						
flexion						greatest
postflexion						
Pacific species						
Sount to anus length/SL						
preflexion						
flexion	shortest					greatest
postflexion						greatest
Snout to first dorsal-fin length/SL						
preflexion						
flexion	shortest					
postflexion						
Body depth/SL						
preflexion						
flexion	smallest					greatest
postflexion						
Snout length/HL						
preflexion		shortest (*T. scepticus**)				
flexion					greatest	
postflexion						
Eye diameter/HL						
preflexion					smallest	greatest
flexion					smallest	greatest
postflexion					smallest	
Atlantic species						
Eye diameter/HL						
preflexion				greatest		
flexion				greatest		
postflexion						
Pectoral-fin length/SL						
preflexion						
flexion					greatest	
postflexion						

Not Present (Pacific species)

Not Present (Atlantic species)

Not Present (*T. scepticus*)

* Due to small sample size of *T. scepticus* larvae, snout length of *T. macellus* not significantly different at P=0.05, but was at P=0.10.

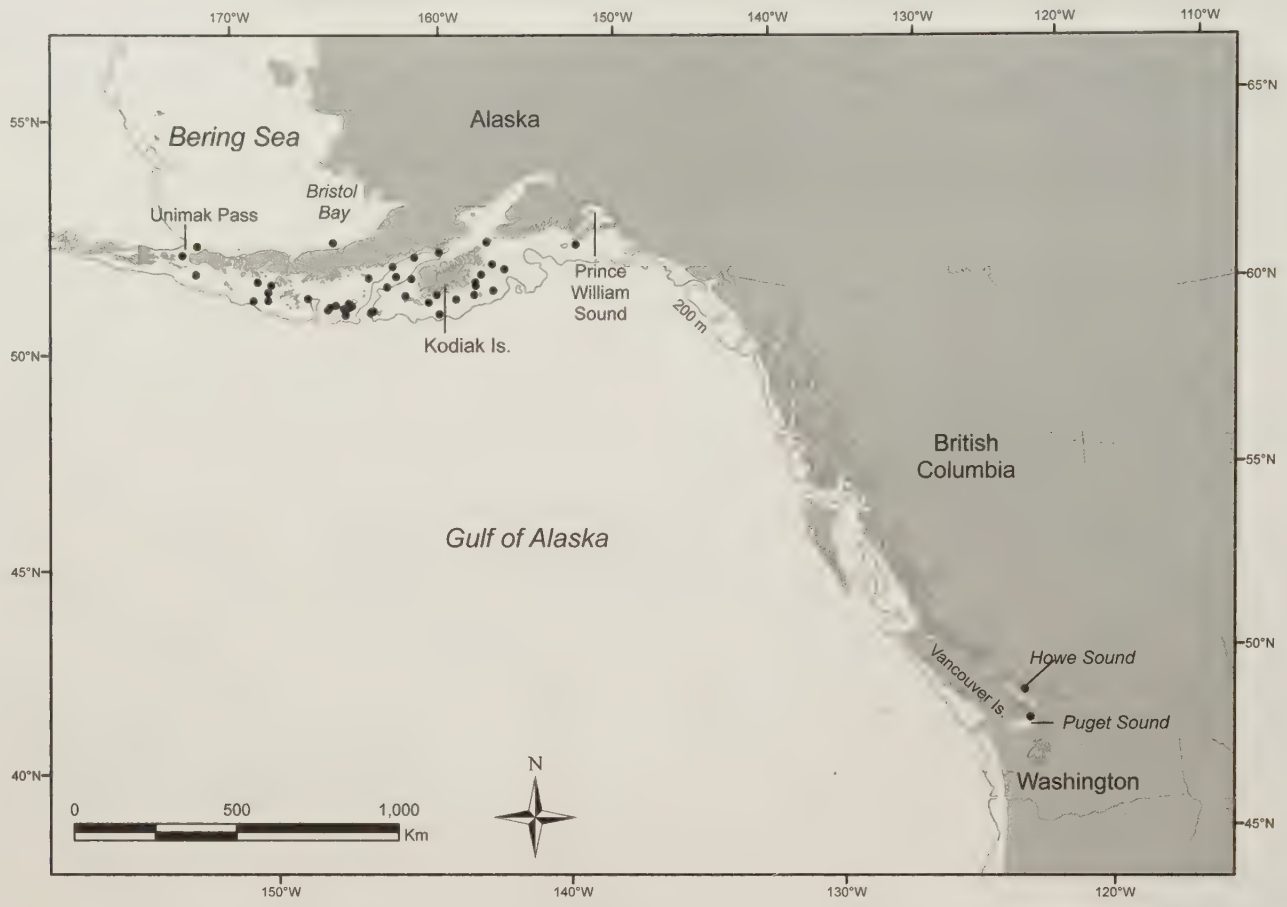

Figure 3

Distribution of all known records, including material examined here, of larvae of *Triglops macellus* in the Bering Sea; Gulf of Alaska; Howe Sound, British Columbia; and Puget Sound, Washington. Each symbol may indicate more than one capture; bathymetry line equals 200 m.

(Appendix 2), and smaller body depth/SL (Appendix 3) than all other flexion stage larvae.

Larvae of *Triglops forficatus* are most similar to those of *T. pingeli*, but have higher counts for vertebrae, dorsal-fin rays, anal-fin rays, and pectoral-fin rays (Table 1). In addition, larvae of *Triglops forficatus* can be differentiated from those of *T. pingeli* by having more pigment on the dorsal surface of the head, possible presence of dorsolateral pigment, no ventrolateral pigment, more pigment on the ventral caudal finfold during the preflexion stage, and more pigment on the base of the caudal-fin rays (Figs. 2 and 12; Table 3).

Triglops macellus, roughspine sculpin (Figs. 3–4)

Material examined. 34 specimens (7.3–20.3 mm SL) examined. Bering Sea: UW 037593, 1 (8.1 mm), 59°40.0′N, 147°40.0′W, 0–110 m depth, bongo net, 22 March 1988. Gulf of Alaska: UW 125844, 1 (9.3 mm), 57°22.0′N, 151°42.0′W, 0–59 m depth, bongo net, 06 May 1972; UW 036117, 1 (20.3 mm), 55°45.7′N, 155°59.3′W, 0–128 m depth, bongo net, 23 May 1983; UW 059540, 1 (19.2 mm), 56°29.6′N, 152°55.0′W, 0–50 m depth, bongo net, 21 May 1982; UW 059949, 1 (19.9 mm), 55°14.1′N, 159°02.0′W, 0–189 m depth, bongo net, 29 May 1982; UW 137136, 2 (8.0–8.2 mm), 57°02.8′N, 154°57.0′W, 0–100 m depth, bongo net, 07 April 1982; UW 039989, 1 (7.3 mm), 56°33.1′N, 154°51.1′W, 0–17 m depth, bongo net, 17 February 1979; UW 125848, 10 (11.8–19.7 mm), 58°20.0′N, 151°28.0′W, 0–74 m depth, Tucker net, 25 May 1986; UW 125845, 2 (10.3–17.2 mm), 56°40.0′N, 153°39.0′W, 0–92 m depth, Tucker net, 27 May 1986; UW 125884, 1 (14.8 mm), 56°55.0′N, 156°19.0′W, 0–159 m depth, Tucker net, 29 May 1986; UW 057199, 1 (9.3 mm), 54°25.2′N, 161°14.0′W, 0–100 m depth, bongo net, 26 March 1981; UW 065112, 1 (9.5 mm), 55°13.5′N, 157°56.0′W, 0–77 m depth, bongo net, 24 April 1981; UW 068831, 1 (11.7 mm), 56°54.8′N, 155°42.0′W,

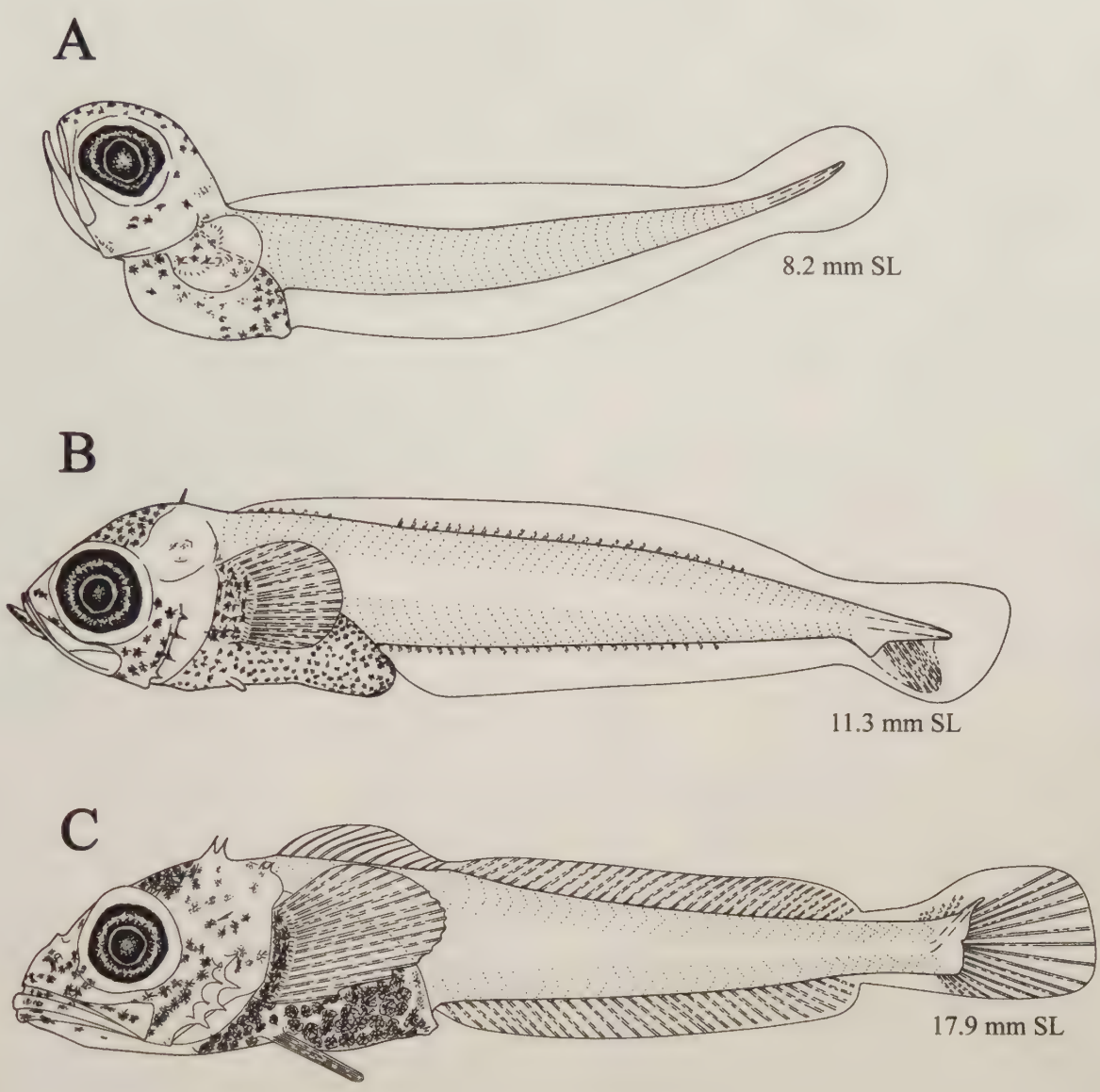

Figure 4

Larvae of *Triglops macellus*: (A) preflexion, 8.2 mm SL (standard length), UW 137136; (B) flexion, 11.3 mm SL, UW 105048; (C) postflexion, 17.9 mm SL, UW 105056. Illustrations by B. Vinter.

0–197 m depth, bongo net, 24 May 1981; UW 125885, 1 (9.6 mm), 56°56.5′N, 153°27.0′W, 0–137 m depth, bongo net, 15 March 1981; UW 125886, 1 (9.6 mm), 55°47.1′N, 155°55.4′W, 0–83 m depth, bongo net, 04 May 1992; UW 125887, 1 (9.4 mm), 57°36.8′N, 151°48.8′W, 0–111 m depth, Tucker net, 08 April 1978; UW 069307, 1 (13.9 mm), 57°57.2′N, 151°47.0′W, 0–31 m depth, Tucker net, 29 March 1978; UW 105048, 1(11.3 mm), 56°32.9′N, 155°52.0′W, 0–108 m depth, Tucker net, 01 June 1989; UW 125888, 1 (9.6 mm), 55°38.4′N, 156°58.8′W, 0–79 m depth, Tucket net, 05 June 1989. British Columbia: UW 105046, 2 (7.3–7.5 mm), 49°29.0′N, 123°18.0′W, depth unknown, gear unknown, 28 December 1984. Puget Sound: UW 125889, 1 (13.8 mm), 48°30.0′N, 122°58.8′W, 0–1 m depth, dip net, 01 April 1980; UW 105056, 1 (17.9 mm), 48°30.0′N, 122°58.8′W, 0–1 m depth, dip net, 07 April 1994.

Occurrence. Adults of *Triglops macellus* are restricted to the Bering Sea and North Pacific Ocean. They are found in the Bering Sea as far north as St. Matthew and

Nunivak islands (about 60°N), in the Aleutian Islands, the Gulf of Alaska to the British Columbia coast, and into Puget Sound, Washington (Pietsch, 1993; Mecklenburg et al., 2002).

Larvae of *Triglops macellus* are found in the southern portion of Bristol Bay in the Bering Sea and Unimak Pass, eastward throughout the northern Gulf of Alaska to Prince William Sound. Larvae are also found farther south in Howe Sound, British Columbia, and Puget Sound, Washington (Fig. 3). Most larvae are collected in May, but they are found in the plankton from February to July over the shelf regions of the eastern Bering Sea and Gulf of Alaska and inshore in Howe Sound, British Columbia and Puget Sound, Washington.

Pigment. Thirty-four larvae were examined to describe changes in pigmentation during development. *Triglops macellus* is identified by heavy head and gut pigment and the absence of postanal pigment (Fig. 4).

Pigment on preflexion larvae is found dorsally on the head from the snout to the posterior margin of the midbrain. Scattered and light internal pigment is present in the otic area and on the nape. A small amount of pigment is present on the jaw angle (Fig. 4A). In the abdominal region, internal pigment covers the dorsal and lateral surfaces of the gut; external melanophores form an oblique row along the anterior margin of the gut and cover the posterior one-third of the ventral surface of the gut. Initially, a few melanophores are present on the pectoral-fin base, isthmus, and the cleithral area under the gill cover; these areas become more heavily pigmented in later preflexion larvae. With development, pigment is visible on the upper jaw and in the area of the preopercle. Pigment on the dorsal surface of the head becomes heavier over the midbrain and in the otic and nape areas. Internal and external pigment on the dorsal rim of the orbit is visible in some specimens. Gut pigment also becomes heavier as melanophores cover all but the anterior half of the ventral surface of the gut.

Head pigment increases in early flexion larvae, appearing on the membrane between the upper jaw and snout, lateral surface of the snout, lower jaw, and along the median cartilage between the dentaries. More pigment is visible in the preopercular region. By about 11 mm SL (Fig. 4B), a small patch of melanophores appears on the head near the otic region; light pigment appears in the opercular area by about 13.5 mm SL. After 14.5 mm SL, nape pigment is more difficult to see as it becomes more deeply embedded. Gut pigment becomes heavier during early flexion and the entire ventral surface of the gut is covered by about 11 mm SL. Pigment appears on the body above the pectoral-fin base after 12.5 mm SL. After 14.5 mm SL, melanophores around the anus become smaller and denser than on the rest of the gut.

In postflexion larvae, pigment on the head increases on the upper jaw, snout, and preopercular area (Fig. 4C). After 19.5 mm SL, fine pigment appears around most of the eye; the ventroposterior quadrant remains unpigmented. Melanophores in the gular region migrate toward the chin after about 20 mm SL. On some specimens a light speckling of pigment on the anterior myomeres dorsal to the pectoral-fin base is visible by 17.5 mm SL; after about 19.5 mm SL this pigment becomes faint. After 19.5 mm SL, pectoral-fin base pigment spreads onto the base of the upper and lower pectoral-fin rays; the central pectoral-fin rays remain unpigmented. Pectoral-fin ray pigment was not visible on the two largest specimens examined (19.9 and 20.3 mm SL).

Proportions. Notochord flexion in *Triglops macellus* begins about 9 mm SL and is complete in most larvae by 17 mm SL. Body depth/SL, head length/SL, snout length/HL, and pectoral-fin length/SL increase throughout development (Table 2). Unlike the previous three body proportions that increase most between preflexion and flexion, pectoral-fin length/SL increases more after flexion. Snout to anus length/SL and snout to first dorsal-fin length/SL increase only between preflexion and flexion stages. Eye diameter/HL and interorbital width/HL both decrease throughout development.

Spination. Two areas of the head have ossified spines in an 11.8 mm SL specimen (early flexion). Two postocular spines are present; the anterior spine is smaller than the posterior spine. Preopercular spines form a double row, the anterior row having three small spines while the posterior row has four larger spines.

By the middle of the flexion stage, or midflexion (13.8 mm SL), parietal and nuchal spines have ossified along with an additional spine on the anterior row of preopercular spines. By postflexion (19.9 mm SL), the parietal and nuchal spines have fused at the base. The single nasal spine, two posttemporal spines, four small pterotic spines, and a supracleithral spine are ossified.

Morphological and other character comparisons. Although there is overlap in some meristic characters, larvae of *Triglops macellus* are distinguished by a vertebral count of 49–51, dorsal-fin rays 28–31, pectoral-fin rays 15–17, heavy head and gut pigment, and a lack of postanal pigment at all stages (Table 3); this combination of characters is unique among the species.

Preflexion larvae of *Triglops macellus* have a significantly shorter snout length/HL than all except larvae of *T. scepticus*; due to the small sample size of two *T. scepticus* larvae, snout length/HL of *T. macellus* was not significantly different at P=0.05, but it was at P=0.10 (Appendix 4). Other morphometric measurements were not significantly different from other species.

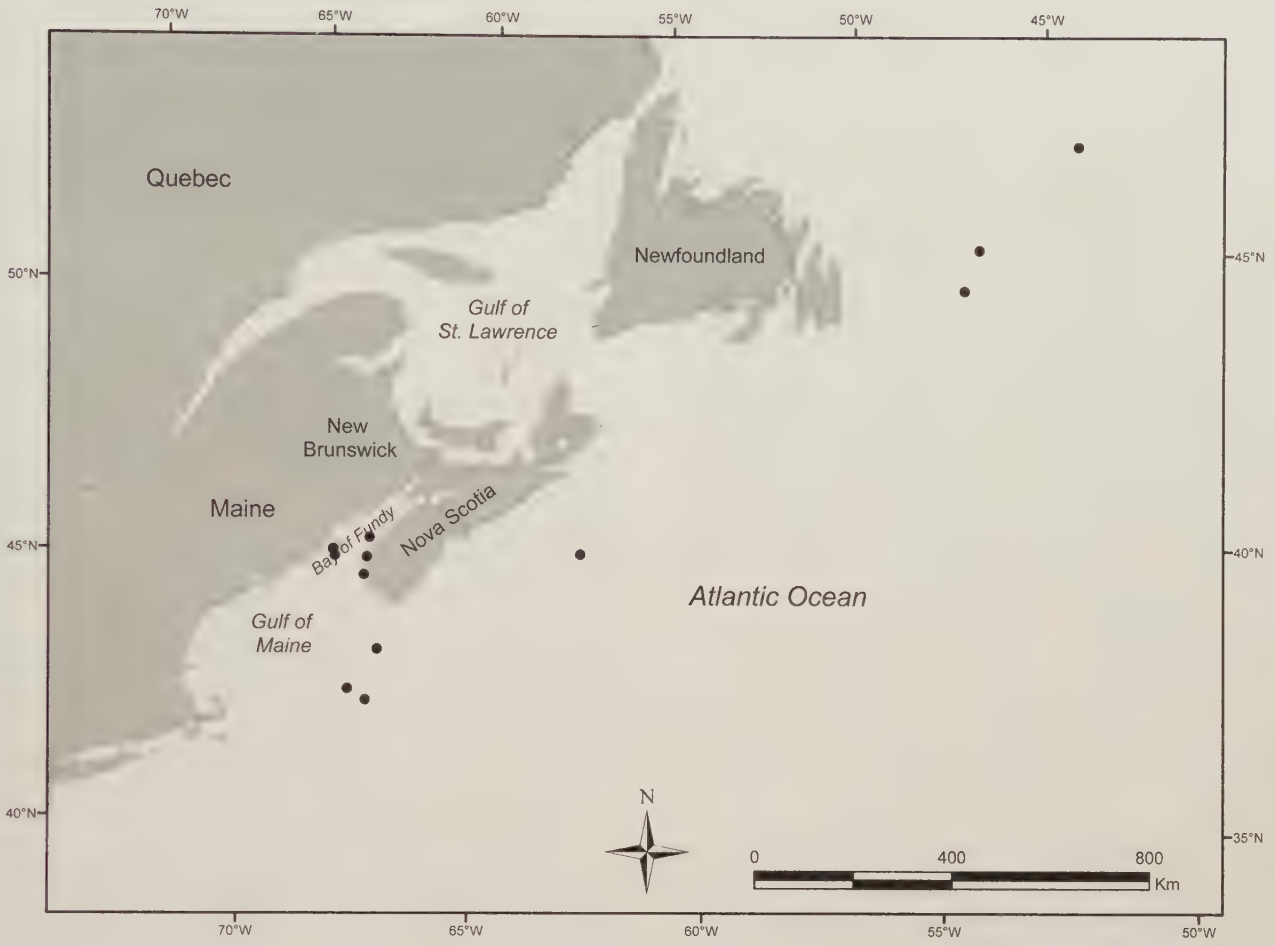

Figure 5

Distribution of material examined of larvae of *Triglops murrayi* from the Bay of Fundy, Nova Scotia, and western North Atlantic Ocean. Each symbol may indicate more than one capture.

Triglops murrayi, moustache sculpin (Figs. 5–6)

Material examined. 18 specimens (9.2–22.6 mm SL) examined. Northwest Atlantic: ARC 9010620, 1 (18.7 mm), 42°00.0′N, 67°00.0′W, 0–62 m depth, bongo net, 10 April 1985; ARC 9010648, 1 (22.6 mm), 42°40.0′N, 66°11.0′W, 0–54 m depth, bongo net, 25 April 1984; ARC 9512315, 1 (21.2 mm), 46°24.0′N, 49°45.4′W, 0–50 m depth, Tucker net, 10 June 1992; ARC 9513006, 1 (13.6 mm), 44°30.0′N, 66°54.5′W, 32–42 m depth, sawtooth bongo net, 14 March 1982; ARC 9513007, 2 (11.2–15.0 mm), 44°30.0′N, 66°54.5′W, 32–42 m depth, bongo net, 14 March 1982; ARC 9513008, 4 (9.6–13.7 mm), 44°37.6′N, 66°56.2′W, 78–80 m depth, sawtooth bongo net, 14 March 1982; ARC 9513009, 5 (10.5–14.3 mm), 44°04.7′N, 66°01.7′W, 27–32 m depth, sawtooth bongo net, 10 March 1983; ARC 9513012, 1 (17.5 mm), 44°36.8′N, 66°55.9′W, 78–81 m depth, bongo net, 08 March 1981; ARC 9513024, 2 (9.2–11.6 mm), 43°45.8′N, 60°56.9′W, 0–43 m depth, Isaacs-Kidd midwater trawl (IKMT) net, 28 January 1981.

Occurrence. Adults of *Triglops murrayi* are restricted to the North Atlantic and Arctic oceans. They are reported from Hudson Bay; near Baffin Island and Ungava Bay, Quebec; and south to Cape Cod, Massachusetts. Eastward, they are found near Greenland, Iceland, Scotland, Spitsbergen, and along the shores of the White Sea (Pietsch, 1993).

Larvae of *Triglops murrayi* examined in this study were collected in the southern extent of their distribution. Larvae of *T. murrayi* are found in the Bay of Fundy and the North Atlantic Ocean south and east of Nova Scotia and east of Newfoundland (Fig. 5). Although larvae are found in the plankton from January to June, most larvae examined were collected in March.

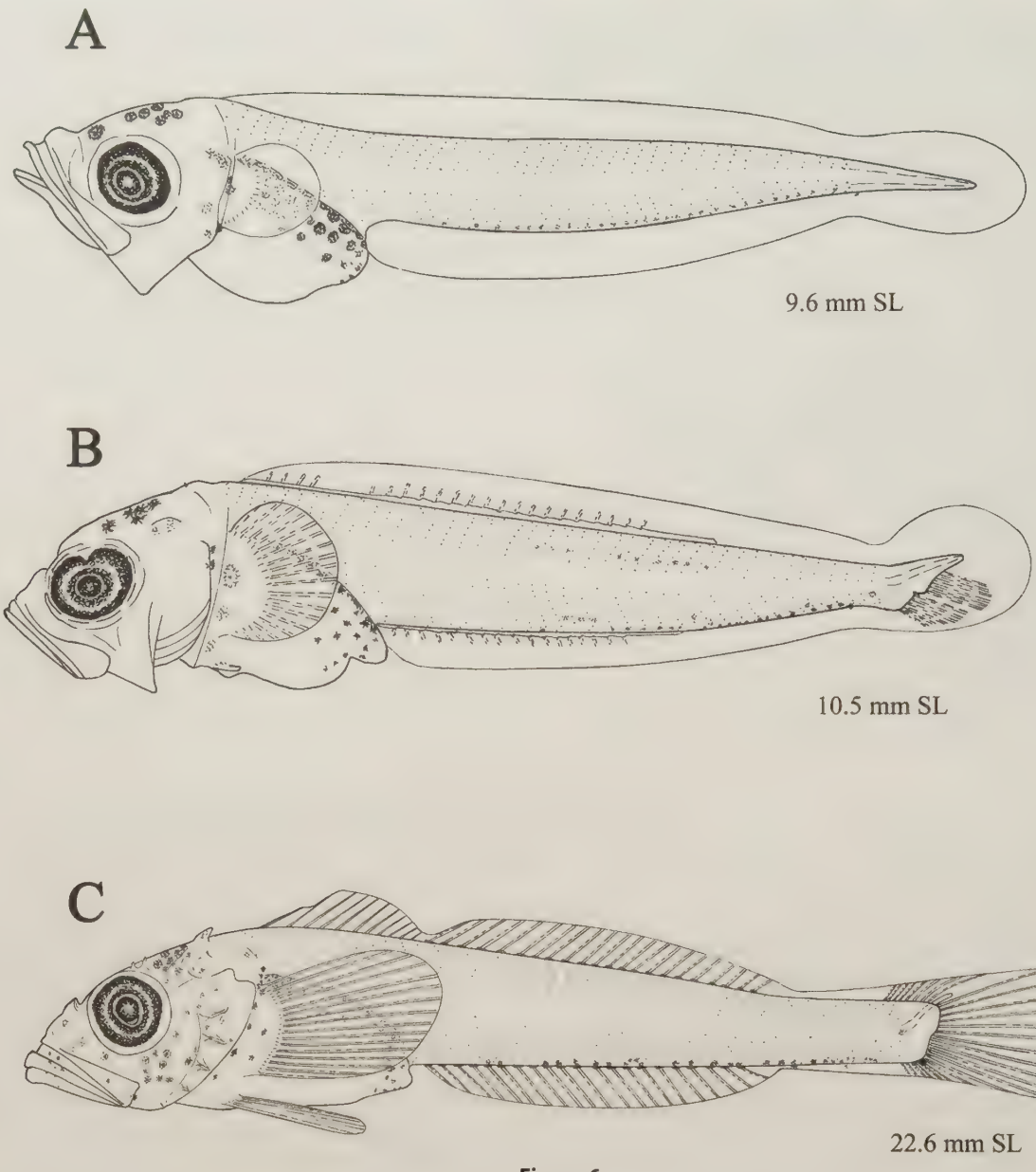

Figure 6

Larvae of *Triglops murrayi*: (A) preflexion, 9.6 mm SL (standard length), ARC 9513008; (B) flexion, 10.5 mm SL, ARC 9513009; (C) postflexion, 22.6 mm SL, ARC 9010648. Illustrations by B. Vinter.

Pigment. Twenty-four larvae were examined to describe changes in pigmentation during development. Larvae of *Triglops murrayi* have moderate pigment on the head and dorsal surface of the gut. Gut pigment includes a concentration of small external melanophores on the lateral and ventral surfaces of the gut near the anus. Postanal pigment comprises a series of 11–26 PVM that become embedded with development and internal dorso- and ventrolateral pigment that is visible in some specimens.

Preflexion larvae have large melanophores on the dorsal surface of the head with most located over the midbrain; 1–2 melanophores are visible over the forebrain and internal pigment is present over the hindbrain (Fig. 6A). Fine pigment is visible on the dorsal rim of the orbit and internal pigment is visible posterior to the eye in the otic region. A single melanophore is present under the gill cover in the cleithral region. Gut pigment is light to moderate with large internal melanophores on the dorsal surface of the gut and external pig-

ment on the dorsolateral surface of the gut. Pigment on the ventral surface of the gut is restricted to a few (2–4) small melanophores near the anus. A series of 19–26 PVM begins 6–11 myomeres posterior to the anus and terminates near the last myomere. These melanophores are spaced approximately one per myomere along the ventral body margin; they may be spaced two per myomere for a short section of the series at about 70% SL. In most specimens, the first one or two melanophores are separated from the rest of the series. Postanal ventral melanophores are embedded and may be difficult to see in some specimens. A single melanophore may be visible on the ventral caudal finfold.

Pigment on or near the head changes little in early flexion larvae (about 10 mm SL), except for the addition of a few melanophores in the cleithral region and margin of the isthmus (Fig. 6B). Several large melanophores develop on the pectoral-fin base. Melanophores around the anus are smaller and finer than those on the dorsal surface of the gut. Postanal ventral melanophores in flexion larvae number 11–25 and begin 6–14 myomeres posterior to the anus. Pigment extends to the last 1–2 myomeres. In some specimens internal pigment on the postanal body appears at this stage; a short row of dorsolateral melanophores, extending from 50% SL to about 75% SL, is visible in addition to several ventrolateral melanophores located just above the PVM beginning at about the middle of the postanal body. Also, a single embedded melanophore is visible in the hypaxial region of the last myomere and 1–2 melanophores are visible on the caudal-fin base where the upper and lower hypural plates meet.

During flexion (10.0–17.6 mm SL), external and internal pigment on the dorsal surface of the head increases. Pigment on the median cartilage between the dentaries is visible in the largest flexion larva (17.6 mm SL). A few melanophores develop in the preopercular region, and pigment in the cleithral region and margin of the isthmus becomes heavier. Melanophores appear on the caudal-fin rays near both of the developing upper and lower hypurals and on the ventral caudal finfold directly below the hypural; one internal melanophore is visible on the caudal peduncle below the notochord.

Postflexion larvae (>18 mm SL) continue to develop more pigment on the head (Fig. 6C). Pigment appears on the lateral surface of the snout, upper and lower jaw, and posterior rim of the orbit. More pigment covers the preopercular region (both internal and external), gular region, isthmus, cleithral region, and pectoral-fin base. Large internal melanophores cover the dorsolateral surfaces of the gut.

Postanal ventral pigment is difficult to see in some postflexion specimens. The number of PVM (21) is similar to that in flexion larvae, but spacing becomes irregular. In larger specimens, only those PVM between the end of the anal fin and beginning of the secondary caudal-fin rays are visible. A light speckling of small melanophores can be seen on the membrane between the upper jaw and snout, nape, on the body over the gut, along the midline at the base of the dorsal-fin spines and rays, on the dorsolateral body at 50% and 75% SL, and on the caudal peduncle. Caudal-fin pigment is restricted to the base of the lower primary caudal-fin rays.

Proportions. Notochord flexion in larvae of *Triglops murrayi* begins after 10 mm SL and is complete by 18 mm SL. Body depth/SL, head length/SL, and pectoral-fin length/SL increase throughout development (Table 2). Unlike body depth/SL and head length/SL, which increase minimally after flexion (2–6% increase), a large increase in pectoral-fin length/SL occurs after flexion (105%). Snout to anus length/SL, snout to first dorsal-fin length/SL, and snout length/HL increase from preflexion to flexion larvae and decrease in postflexion. Eye diameter/HL and interorbital width/HL both decrease throughout development.

Spination. Single parietal and nuchal spines, four posterior preopercular spines, and two small postocular spines are ossified by 14.3 mm SL.

Morphological and other character comparisons. Meristic counts for the three species found in the western North Atlantic Ocean (*Triglops murrayi*, *T. nybelini*, and *T. pingeli*) overlap to a greater degree than those for species in the North Pacific Ocean and Bering Sea. *Triglops murrayi* have fewer anal-fin rays than *T. nybelini* and fewer dorsal-fin rays with minimal overlap. The low end of the range for dorsal- and anal-fin rays for *T. murrayi* is lower than for *T. pingeli*, but counts do overlap at the top of the range (D:23–24, A:21–23; Pietsch, 1993). *Triglops murrayi* usually has fewer PVM than *T. pingeli* at all stages of development and usually has fewer PVM than *T. nybelini* during preflexion stage (Table 3). In addition, *T. murrayi* has a short line of dorsolateral pigment during flexion stage, and large melanophores on the pectoral-fin base.

Morphological comparisons of larvae of *Triglops murrayi* with all species resulted in a significant difference for only one measurement: flexion larvae of *T. murrayi* have a significantly greater snout length/HL than all except larvae of *T. pingeli*. Larvae of *T. murrayi* are most similar to *T. pingeli* and they may be difficult to distinguish from each other. Preflexion and early flexion larvae of *T. murrayi* have large melanophores on the pectoral-fin base, whereas similar stages of *T. pingeli* have no pigment or only small melanophores in that area. Also, flexion larvae of *T. murrayi* have a significantly shorter pectoral-fin length/SL than *T. pingeli* (Appendix 5).

Figure 7

Distribution of material examined of larvae of *Triglops nybelini* from the Gulf of Maine and western North Atlantic Ocean. Each symbol may indicate more than one capture.

Triglops nybelini, bigeye sculpin (Figs. 7–9)

Material examined. Five specimens (8.0–14.4 mm SL) examined. Northwest Atlantic: ARC 9010624, 1 (11.5 mm), 47°00.0′N, 44°30.0′W, 0–110 m depth, bongo net, 11 April 1980; ARC 9513011, 1 (8.6 mm), 43°31.4′N, 66°18.5′W, 75–79 m depth, bongo net, 05 March 1981; ARC 9010634, 1 (14.4 mm), 47°00.0′N, 45°00.0′W, 0–148 m depth, bongo net, 06 May 1981; ARC 9513001, 1 (8.0 mm), 43°56.5′N, 66°24.9′W, 0–57 m depth, sawtooth bongo net, 13 March 1982; ARC 9010623, 1 (10.1 mm), 47°00.0′N, 45°00.0′W, 0–140 m depth, bongo net, 13 March 1983.

Occurrence. Adults of *Triglops nybelini* are found in the North Atlantic Ocean and are nearly circumpolar in the Arctic Ocean. They are found in the Beaufort Sea; east to Baffin Island and Ungava Bay, Quebec; off Labrador and the west coast of Greenland; to Spitsbergen and the Barents, Kara, and Laptev seas (Pietsch, 1993).

Larvae of *Triglops nybelini* examined in this study were collected farther south than their reported adult distribution. *Triglops nybelini* larvae are uncommon in collections; specimens used in this study were found in the Gulf of Maine and in the North Atlantic Ocean east of Newfoundland (Fig. 7) and were collected from March to May.

Pigment. Five larvae (preflexion and flexion) were available to examine for changes in pigmentation during development. Larvae of *Triglops nybelini* have moderate pigment on the head and moderate to heavy pigment on the dorsal surface of the gut. Postanal pigment comprises a series of 20–45 PVM that become embedded with development, internal dorsal notochord pigment, internal ventrolateral pigment above the PVM, and dorsal midline pigment that is first visible in flexion specimens.

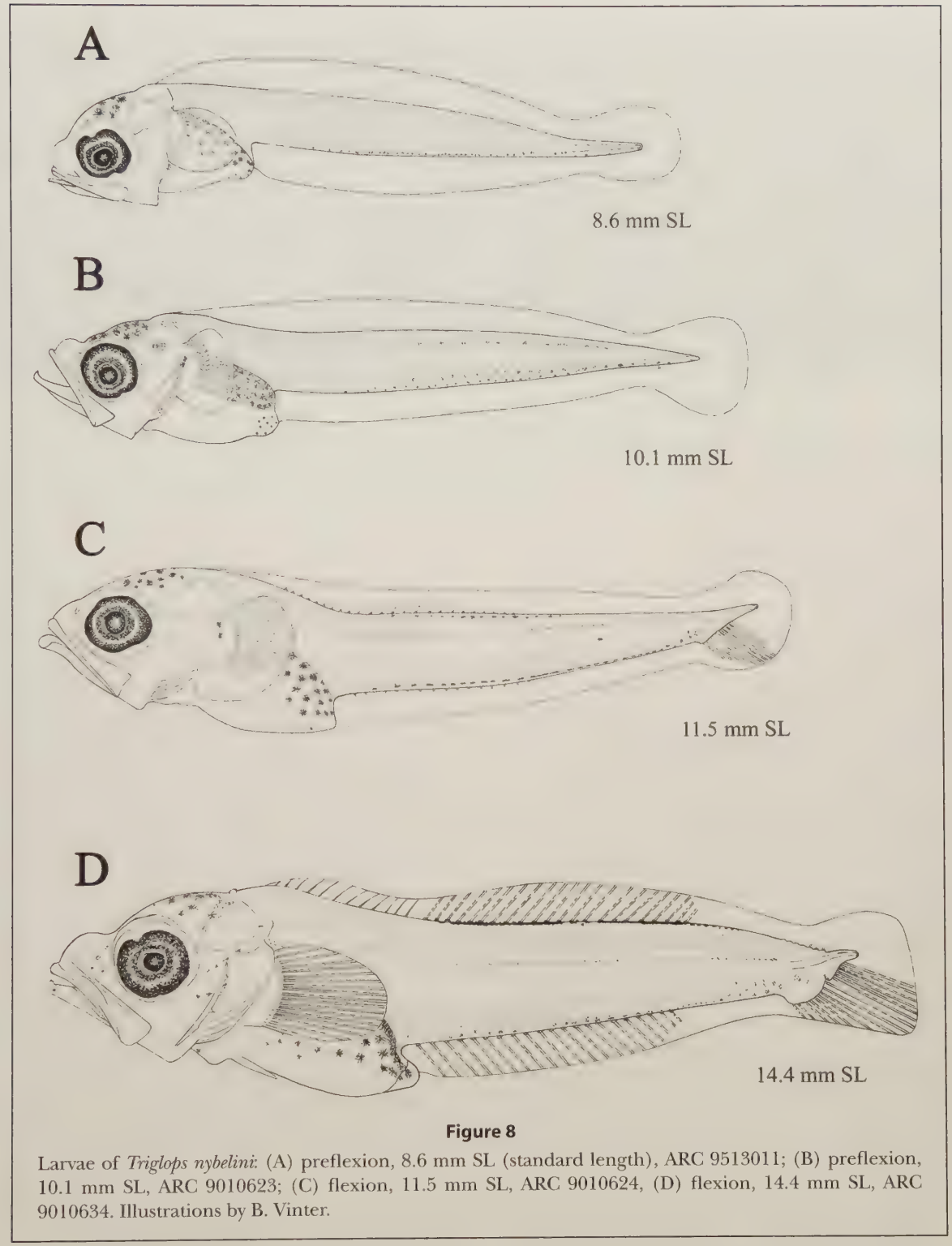

Figure 8

Larvae of *Triglops nybelini*: (A) preflexion, 8.6 mm SL (standard length), ARC 9513011; (B) preflexion, 10.1 mm SL, ARC 9010623; (C) flexion, 11.5 mm SL, ARC 9010624, (D) flexion, 14.4 mm SL, ARC 9010634. Illustrations by B. Vinter.

Head pigment in early preflexion larvae (8.0 mm SL) is moderate. Large external melanophores are on the dorsal surface of the head over the forebrain and midbrain and small internal melanophores are visible on the midbrain. A large internal melanophore is visible behind the eye in the otic area and a single external melanophore is present on the nape. Pigment on the gut is moderate and restricted to the dorsolateral surface. Postanal ventral melanophores are present starting at nine myomeres posterior to the anus; there are 45 PVM, anteriorly spaced one spot per myomere. At 50% SL, spacing changes to one or two per myomere

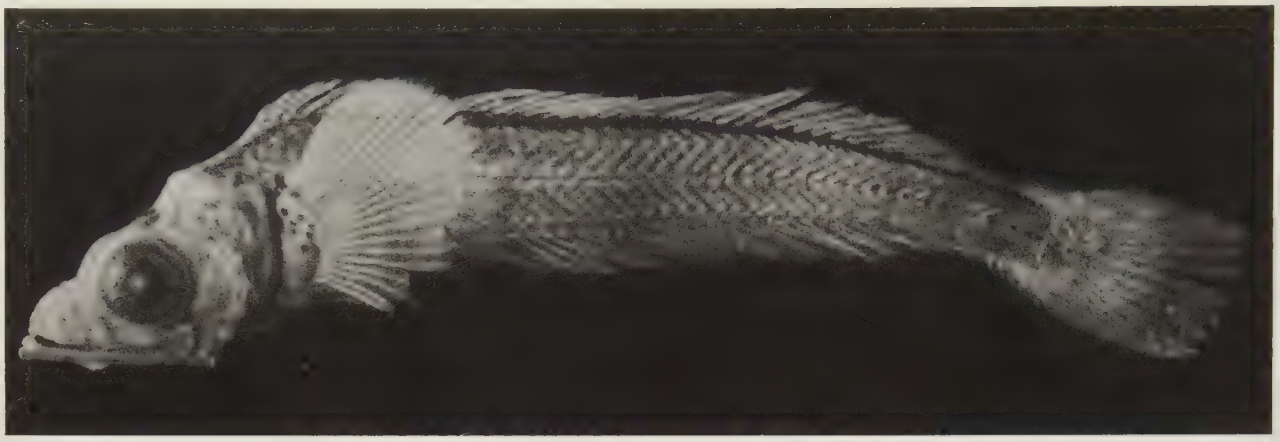

Figure 9

Photograph of *Triglops nybelini*, 27 mm SL (standard length), collected by plankton net at 30 m depth in Ungava Bay, Quebec, Canada (Dunbar and Hildebrand, 1952 - reverse image of the original).

and the series terminates near the last myomere. A few melanophores are present on the ventral caudal finfold in some larvae.

With development, more pigment is visible on the nape and pigment appears in the cleithral area (Fig. 8A). Pigment covers the upper half of the gut and small melanophores are present on the ventral surface of the gut near the anus. Internal dash-like pigment is visible above the notochord starting at 50% SL and terminating at 90% SL. Beginning six myomeres posterior to the anus, 38 PVM are spaced one per myomere along their entire length. Postanal ventral melanophores extend onto the ventral caudal margin beyond the last myomere, and there is one melanophore on the ventral caudal finfold.

Head pigment in the largest preflexion larva covers the entire dorsal surface of the head over the forebrain and midbrain (Fig. 8B). Nape pigment becomes embedded and is more difficult to see. Two pigment spots are present on the pectoral-fin base. Pigment on the dorsolateral surface of the gut is heavy. Internal pigment above the notochord is visible, starts at approximately 50% SL, and terminates at the next to last myomere; these melanophores are more widely spaced anteriorly and more closely spaced posteriorly. Postanal ventral melanophores (22) begin 10 myomeres posterior to the anus. Those PVM located on the posterior myomeres and extending onto the ventral caudal margin and finfold appear to be darker than other PVM. Additional internal pigment located just above the PVM begins at approximately 50% SL and ends at approximately 90% SL.

The only additional anterior pigment visible in early flexion is located on the isthmus near the jaw angle and therefore is not visible except when viewed ventrally. Dorsal midline pigment has developed, beginning at about 50% SL and terminating at 75% SL (Fig. 8C). Melanophores are spaced about one per myomere and are irregular in size. Internal pigment above the notochord extends further anteriorly, starting about two myomeres posterior to the anus. Beginning four myomeres posterior to the anus are 30 PVM. These melanophores are dash-like and located close together; at 70% SL they appear to be a solid line. Multiple ventrolateral melanophores are present anterior to the developing caudal fin and there is one mediolateral spot located at 75% SL.

More areas of the head are pigmented in midflexion (Fig. 8D). Light pigment is visible on the membrane between the upper jaw and snout, snout (internal), dorsal rim of the orbit, chin, and the ventral edge of the dentary anterior to the jaw angle. A light speckling of pigment on the preopercular area behind the eye and additional pigment on the isthmus is present. Dorsolateral gut pigment extends over most of the gut wall and no pigment is present on the ventral surface of the gut.

Dorsal midline pigment begins just posterior to the first dorsal-fin ray and ends about five myomeres anterior to the developing caudal fin. The melanophores are spaced closely together, forming a solid line until the last dorsal-fin ray, at which point they are constricted and separate. Internal pigment above the notochord begins at about 30% SL and ends near the last myomere anterior to the caudal fin.

Postanal ventral melanophores (20) begin four myomeres posterior to the anus and terminate about four myomeres anterior to the developing lower hypural plate. The series, which is becoming embedded, is spaced one melanophore per myomere to about 60% SL and skips three myomeres. At about 65% SL, PVM

are dash-like and appear as a solid line at 75% SL when viewed ventrally; when viewed laterally, melanophores look like a number of dashes until 80–90% SL where they appear as very small spots. More internal pigment above the PVM is present near the caudal peduncle.

Internal pigment is present on the developing lower hypural plate; external pigment is present near the distal margin at the point where the upper and lower hypural plates meet. Caudal-fin ray pigment is restricted to a few melanophores on the upper caudal-fin rays near the caudal margin.

Proportions. Notochord flexion in larvae of *Triglops nybelini* begins between 10.0 and 11.5 mm SL; the largest larva examined (14.4 mm SL) was in late flexion stage. All proportions except for eye diameter/HL and interorbital width/HL increase from preflexion to flexion stage (Table 2). The greatest increases in morphometric measurements between preflexion and flexion stages are in snout to first dorsal-fin length/SL (39.7%), body depth/SL (43.9%), and pectoral-fin length/SL (57.1%).

Spination. There were too few specimens to determine ossification of spines through clearing and staining. A single row of three preopercular spines was present on the largest larva (14.4 mm SL), in addition to single parietal, nuchal, posttemporal, and supracleithral spines. Postocular spines were not visible.

Morphological and other character comparisons. Most meristic counts for *Triglops nybelini* overlap those for *T. murrayi* and *T. pingeli*, the other species co-occurring in the western North Atlantic Ocean. *Triglops nybelini* has more anal-fin rays than *T. murrayi*; soft dorsal-fin and pectoral-fin ray counts are also higher with minimal overlap (Pietsch, 1993). Although there is some overlap, *T. nybelini* usually has a higher number of anal-fin rays, soft dorsal-fin rays, and pectoral-fin rays than *T. pingeli* (Pietsch, 1993). In addition, internal ventrolateral pigment above the PVM on preflexion larvae and internal dorsal notochord pigment set *T. nybelini* apart. Flexion larvae of *T. nybelini* have pigment along the dorsal midline at the base of the dorsal-fin rays. As shown in the photograph of a 27-mm SL postflexion larva collected from Ungava Bay by Dunbar and Hildebrand (1952) (Fig. 9), this dorsal midline pigment becomes heavier with development.

Prior to the development of the full complement of fin rays, the eye diameter/HL of pre- and early flexion larvae of *T. nybelini* is significantly larger than those of its Atlantic congeners (Appendices 6–7).

Triglops pingeli, ribbed sculpin (Figs. 10–12)

Material examined. 45 specimens (6.1–28.5 mm SL) examined. Northwest Atlantic: ARC 9010640, 1 (7.4 mm), 41°41.6′N, 66°03.1′W, 0–93 m depth, Isaacs-Kidd midwater trawl (IKMT) net, 12 January 1982; ARC 9010662, 1 (10.1 mm), 43°45.0′N, 66°25.0′W, 0–126 m depth, bongo net, 03 March 1984; ARC 9010669, 1 (7.5 mm), 44°21.0′N, 63°37.0′W, 97–99 m depth, IKMT, 23 January 1979; ARC 9010700, 1 (7.1 mm), 43°03.4′N, 64°02.1′W, 0–90 m depth, IKMT, 26 January 1982; ARC 9010703, 1 (6.2 mm), 42°06.4′N, 67°01.8′W, 0–56 m depth, IKMT, 13 January 1982; ARC 9513004, 1 (8.3 mm), 44°05.4′N, 66°16.1′W, 27–32 m depth, sawtooth bongo net, 14 March 1982; ARC 9513013, 1 (8.5 mm), 43°30.6′N, 66°20.5′W, 0–95 m depth, bongo net, 10 February 1981; ARC 9513016, 1 (7.7 mm), 44°58.0′N, 61°20.0′W, depth unknown, IKMT, 16 February 1977; ARC 9513026, 1 (6.8 mm), 45°01.0′N, 57°50.3′W, 0 m depth, sawtooth bongo net, 23 January 1981; ARC 9513027, 1 (6.7 mm), 41°13.0′N, 60°12.4′W, 0 m depth, sawtooth bongo net, 28 January 1981; ARC 9513028, 1 (9.0 mm), 43°08.9′N, 65°53.7′W, 0 m depth, sawtooth bongo net, 10 February 1981; ARC 9010658, 2 (8.0–10.8 mm), 41°46.0′N, 66°39.0′W, 0–59 m depth, bongo net, 17 February 1985; ARC 9513006, 1 (10.0 mm), 44°30.0′N, 66°54.5′W, 32–42 m depth, sawtooth bongo net, 14 March 1982; ARC 9513008, 2 (10.2–10.7 mm), 44°37.6′N, 66°56.2′W, 78–80 m depth, sawtooth bongo net, 14 March 1982; ARC 9513009, 2 (10.9–12.5 mm), 44°04.7′N, 66°15.7′W, 27–32 m depth, sawtooth bongo net, 10 March 1983; ARC 9513024, 3 (8.0–9.8 mm), 43°45.8′N, 60°56.9′W, 0–43 m depth, IKMT, 28 January 1981. Beaufort Sea: ARC 9010608, 1 (28.5 mm), 69°39.0′N, 125°35.0′W, depth unknown, gear unknown, 01 August 1963. Bering Sea: UW 125993, 1 (16.6 mm), 53°57.0′N, 166°37.0′W, 0–2 m depth, Tucker net, 04 June 1986; UW 125994, 1 (18.2 mm), 54°15.8′N, 165°49.6′W, 0–69 m depth, bongo net, 16 April 1993; UW 125995, 1 (14.3 mm), 55°16.9′N, 163°20.3′W, 0–34 m depth, bongo net, 20 May 1976; UW 037858, 1 (12.5 mm), 54°45.0′N, 164°55.0′W, 0–55 m depth, bongo net, 11 April 1988. Gulf of Alaska: UW 052327, 1 (9.5 mm), 57°11.2′N, 154°49.6′W, 0–75 m depth, bongo net, 14 April 1989; UW 105068, 2 (16.4–17.1 mm), 55°21.0′N, 159°46.0′W, 0–74 m depth, Tucker net, 30 May 1986; UW 125996, 1 (11.8 mm), 56°30.0′N, 155°14.0′W, 0–23 m depth, bongo net, 18 March 1981; UW 125997, 1 (16.3 mm), 57°22.0′N, 151°42.0′W, 0–59 m depth, bongo net, 06 May 1972; UW 125998, 1 (15.3 mm), 57°40.7′N, 152°07.4′W, 0–146 m depth, IKMT, 07 April 1978; UW 032200, 1 (12.1 mm), 57°16.0′N, 152°55.0′W, 0–90 m depth, Tucker net, 05 April 1978; UW 032202, 1 (12.9 mm), 57°16.0′N, 152°55.0′W, 0–50 m depth, Tucker net, 14 April 1978; UW 032203, 1 (9.8 mm), 58°10.0′N, 152°14.0′W, 0–90 m depth, Tucker net, 21 April 1978; UW 032204, 1 (11.2 mm),

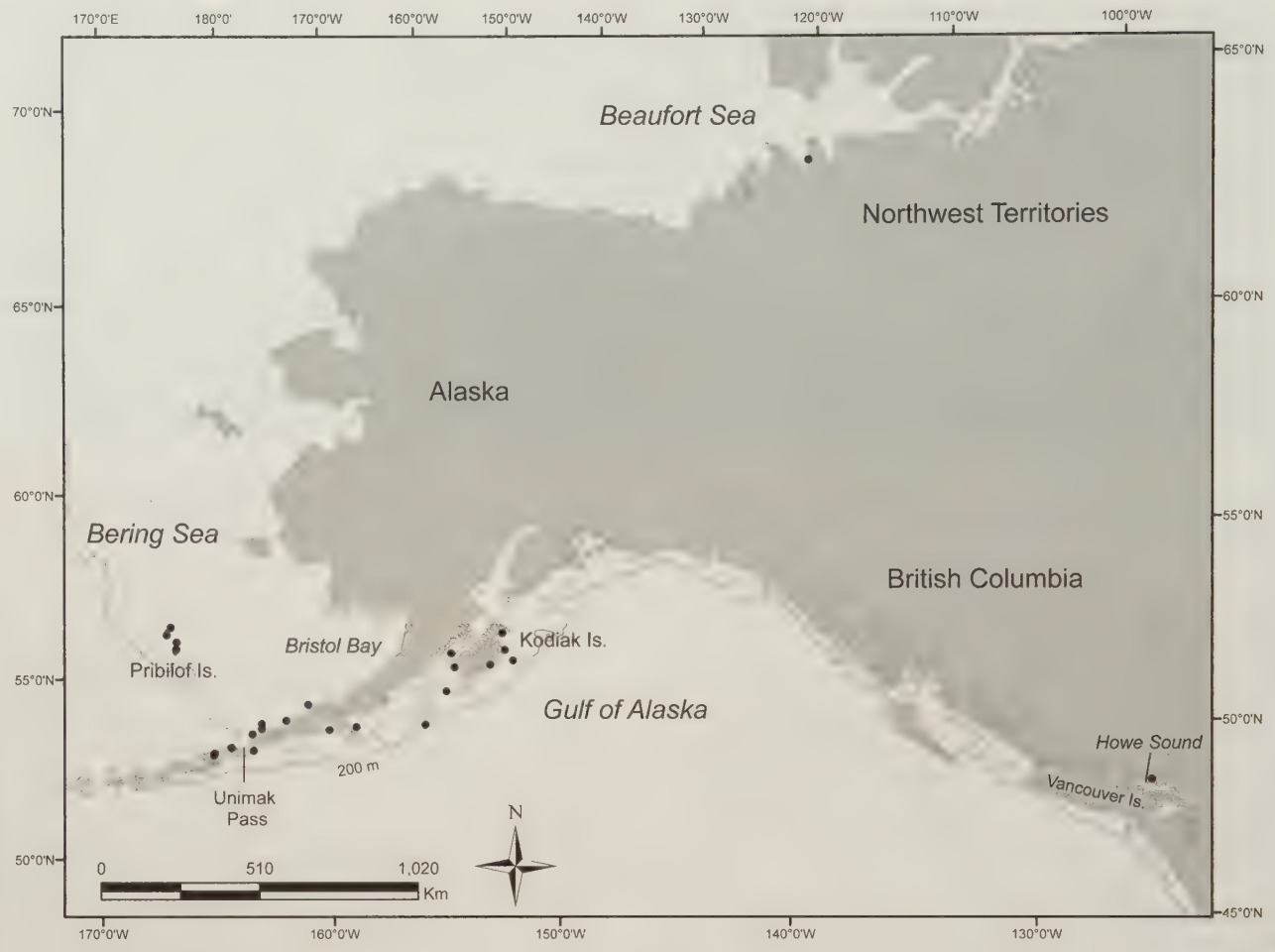

Figure 10

Distribution of all known records, including material examined here, of larvae of Pacific *Triglops pingeli* in the Beaufort Sea; Bering Sea; Gulf of Alaska; and Howe Sound, British Columbia. Each symbol may indicate more than one capture; bathymetry line equals 200 m.

57°16.0′N, 152°55.0′W, 0–100 m depth, Tucker net, 15 March 1979; UW 032205, 1 (10.8 mm), 57°16.0′N, 152°55.0′W, 0–30 m depth, Tucker net, 15 March 1979; UW 032206, 1 (8.9 mm), 58°10.0′N, 152°14.0′W, 0–10 m depth, Tucker net, 06 March 1979. British Columbia: UW 125835, 1 (6.9 mm), 49°29.0′N, 123°18.0′W, depth unknown, gear unknown, 28 December 1984; UW 125846, 1 (7.1 mm), 49°29.0′N, 123°18.0′W, depth unknown, gear unknown, 28 December 1984; UW 105065, 3 (6.1–6.5 mm), 49°29.0′N, 123°18.0′W, depth unknown, gear unknown, 09 February 1985; UW 125992, 2 (6.4–6.5 mm), 49°29.0′N, 123°18.0′W, depth unknown, gear unknown, 20 March 1987.

Occurrence. *Triglops pingeli* is the most wide-ranging species of the genus, found throughout coastal waters of the Arctic, North Pacific, and Atlantic oceans. Adults have been reported in the Sea of Japan, Sea of Okhotsk, Bering Sea, eastern Aleutian Islands, Gulf of Alaska, and south to Puget Sound, Washington. Northward, they are found in the Chukchi and Beaufort seas; eastward to the Queen Elizabeth Islands, Hudson Bay, Baffin Island; south to Cape Cod, Massachusetts; to Greenland and Spitsbergen, and the Barents, Kara, and Laptev seas (Pietsch, 1993; Mecklenburg et al., 2002).

Of the Pacific species of *Triglops* larvae, *T. pingeli* are the most widespread. They are found from the Beaufort Sea; Pribilof Islands; west of Unimak Pass eastward to around Kodiak Island; and to Howe Sound on the east side of Vancouver Island, B.C. (Fig. 10). They are collected from January to September.

Compared with other species of the Atlantic group, larvae of *T. pingeli* are common and found in eastern Hudson Bay, the Atlantic Ocean east of Cape Cod, Gulf

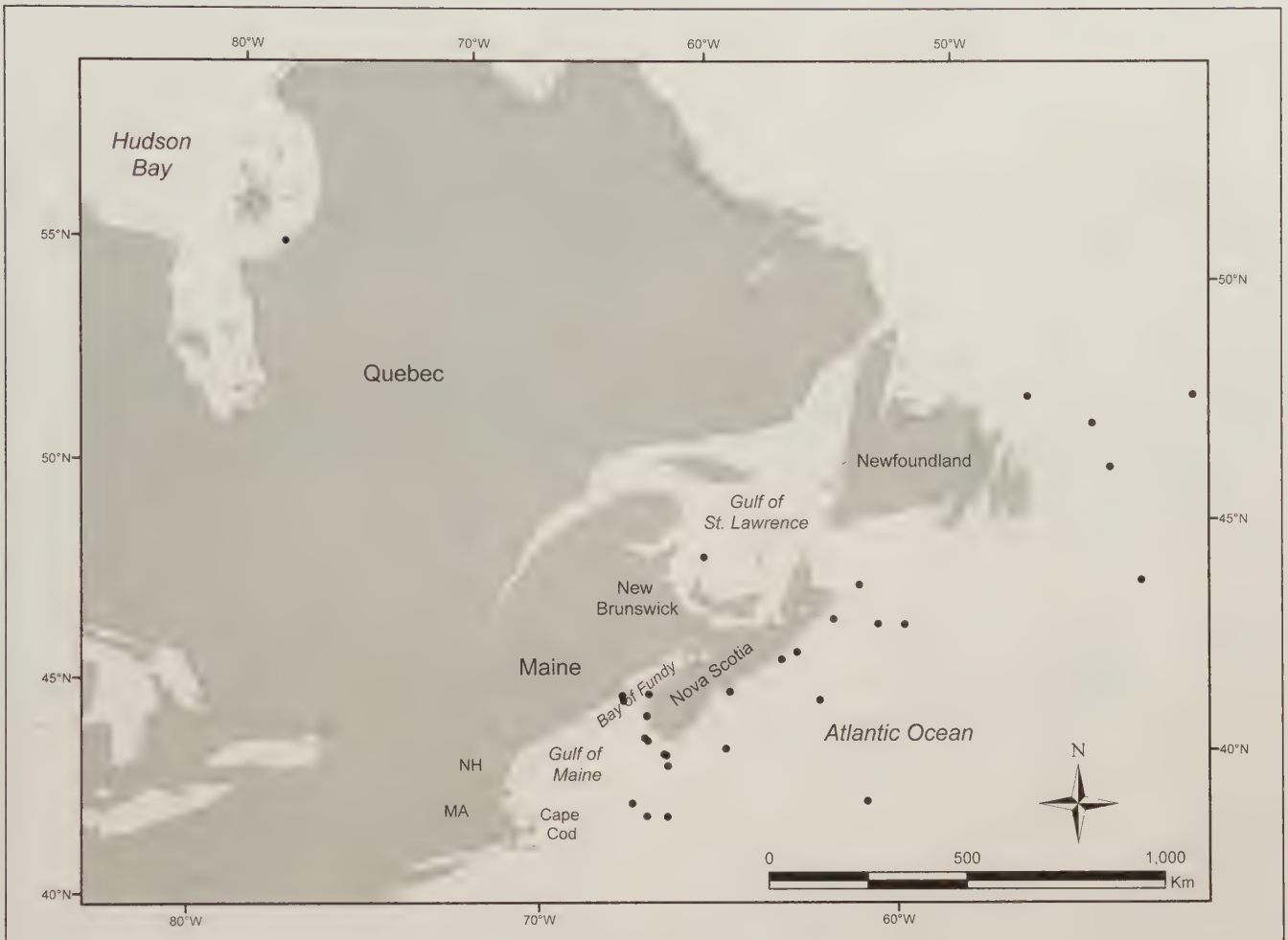

Figure 11

Distribution of material examined of larvae of Atlantic *Triglops pingeli* from Hudson Bay and Gulf of St. Lawrence, Quebec; Gulf of Maine, Bay of Fundy, Nova Scotia; and western North Atlantic Ocean. Each symbol may indicate more than one capture.

of Maine and northward into the Bay of Fundy, east of Nova Scotia and into the Gulf of St. Lawrence, and to the east off Newfoundland (Fig. 11). Larvae are collected from January to March.

Pigment. Forty-five larvae were examined to describe changes in pigmentation during development. Larvae of *Triglops pingeli* have moderate head and gut pigment. Gut pigment includes large internal dorsal melanophores and a concentration of small external melanophores on the lateral and ventral surfaces of the gut near the anus. Postanal pigment is composed of a series of PVM (yolk-sac larvae, 60–85; preflexion-postflexion larvae, 23–49) that decrease in number and become embedded with development.

Head pigment in yolk-sac larvae is light and is located over the midbrain and nape (Fig. 12A). Gut pigment is light with internal melanophores on the mid-lateral and dorsal surface of the gut; pigment on the ventral surface of the gut is restricted to the anterior margin of the gut and anus. A series of 60–85 PVM begins 6–7 myomeres posterior to the anus, spaced 2–3 per myomere; an additional 5–6 melanophores extend onto the ventral margin of the notochord.

Head pigment in preflexion larvae is moderate; most is located over the midbrain and nape with 1–2 melanophores over the forebrain (Fig. 12B). Fine pigment is visible on the dorsal rim of the orbit and internal pigment is visible in the otic region on some specimens. A few melanophores are present on the cleithral region under the gill cover. Gut pigment is moderate with internal melanophores on the dorsal surface of the gut and external pigment extending to the mid-lateral surface. Pigment on the ventral surface of the gut is restricted to its ante-

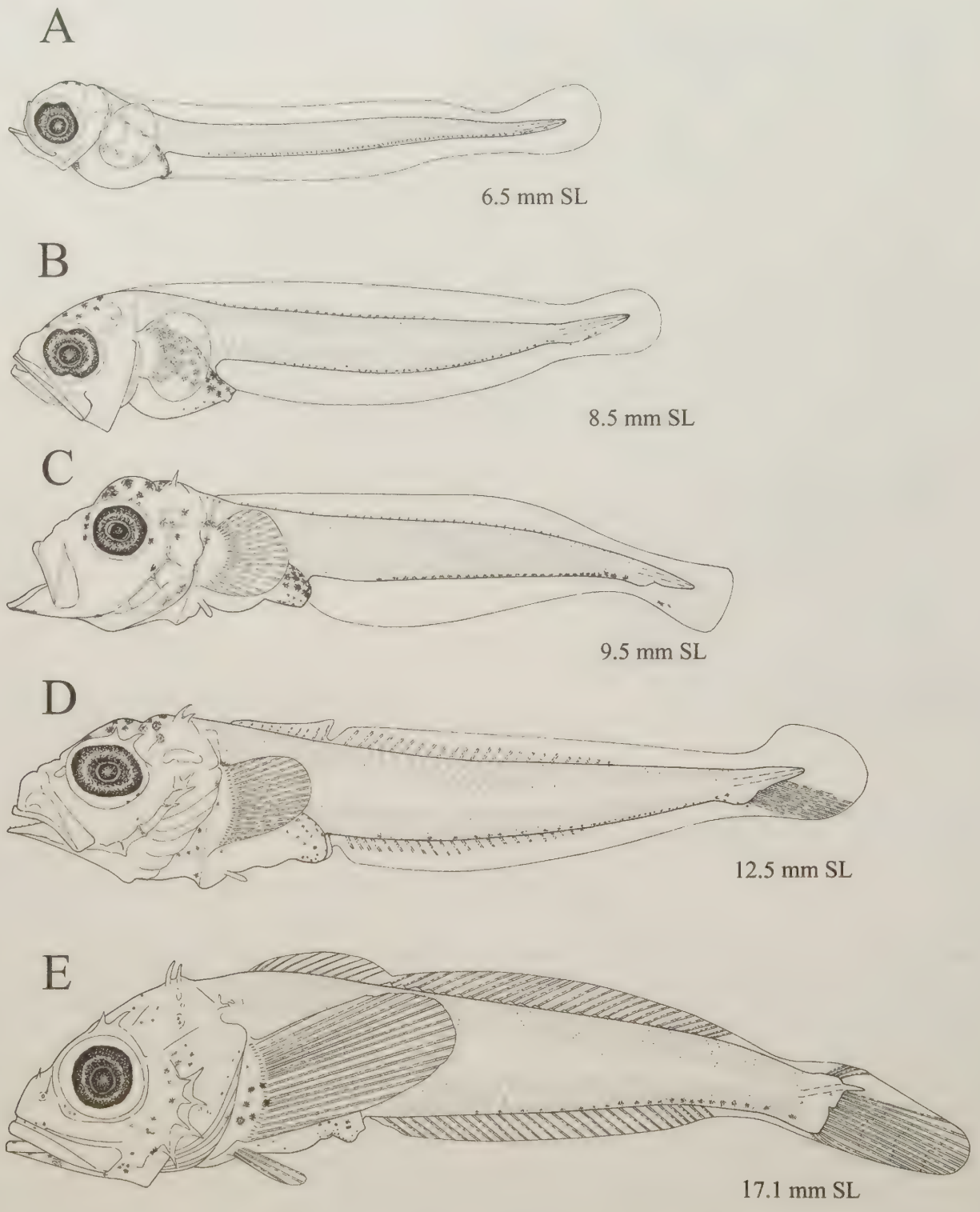

Figure 12

Larvae of *Triglops pingeli*: (A) yolk-sac, 6.5 mm SL (standard length), UW 105065; (B) preflexion, 8.5 mm SL, ARC 9513013; (C) preflexion, 9.5 mm SL, UW 052327; (D) flexion, 12.5 mm SL, UW 037858; (E) postflexion, 17.1 mm SL, UW 105068. Illustrations by B. Vinter.

rior margin and a few (2–4) small melanophores near the anus. A series of 30–49 PVM begins 6–10 myomeres posterior to the anus and terminates at the last myomere. These melanophores are spaced approximately one per myomere along the anterior half of the series and 1–2 per myomere along the posterior half. This series is embedded and is at times difficult to see. Additional internal postanal pigment is visible in some specimens, appearing as an irregular row directly above the PVM. Pigment in the caudal area consists of 1–2 melanophores near the ventral caudal margin and a single melanophore on the ventral caudal finfold in some specimens.

Head pigment increases in late preflexion larvae. Melanophores appear dorsally on the snout, in front of the eye, and on the preopercular region posterior to the eye (Fig. 12C). Light pigment is visible on the chin and on the lower jaw near the jaw angle. Nape pigment becomes embedded and difficult to see. Late preflexion larvae have fewer PVM than early preflexion larvae (Fig. 12B).

Pigment is visible in some flexion larvae on the median cartilage between the dentaries. A few melanophores develop on the isthmus, pectoral-fin base, and cleithral area (Fig. 12D). Melanophores around the anus are smaller and finer than those on the dorsal surface of the gut. A series of 23–38 PVM in flexion larvae begins 4–9 myomeres posterior to the anus. Melanophores in the anterior half of the series are more widely and irregularly spaced, and more difficult to see than are those in the posterior half. Pigment extends to the last 1–2 myomeres; additional pigment (1–2 melanophores) is visible on the ventral margin of the hypural plate and ventral caudal finfold. Pigment may be visible on the caudal-fin base and bases of the developing caudal-fin rays.

Although the degree of pigmentation may vary greatly among specimens, postflexion larvae have less pigment on the crown, developing more pigment on other areas of the head (Fig. 12E). The preopercular region (with both internal and external melanophores), sides of the snout, lower jaw, and gular region are more heavily pigmented. Additional pigment appears on the anterior and posterior rims of the orbit, isthmus, in the cleithral region under the gill cover, and on the pectoral-fin base. Large internal melanophores cover most of the dorsal and lateral surfaces of the gut, and the ventral surface of the gut develops additional fine external pigment anterior to the anus. Postanal ventral pigment, beginning 5–9 myomeres posterior to the anus, is more difficult to see in some specimens, especially in the anterior section of the series. The number of PVM (23–34) and their spacing is similar to those in flexion larvae; however, pigment at the end of the series is slightly above the ventral midline. Pigment on the caudal-fin base is located below and sometimes adjacent to the notochord. Caudal-fin ray pigment, when present, is generally restricted to the lower half of the fin.

Proportions. Notochord flexion in larvae of *Triglops pingeli* begins about 9.8 mm SL and is complete by about 15 mm SL. Snout to anus length/SL, snout to first dorsal length/SL, and head length/SL increase at similar rates with development (Table 2). Body depth/SL and pectoral-fin length/SL also increase throughout development, but at much greater rates. Snout length/HL increases mostly from preflexion to flexion larvae. Eye diameter/HL and interorbital width/HL decrease throughout development.

Spination. Spines are ossified by early flexion (9.8 mm SL). Parietal, nuchal, and posttemporal spines are single; one or two postocular spines are present, with most of our specimens possessing two spines. Preopercular spines form a double row with three spines in the anterior row and four spines in the posterior row.

In the postflexion specimen examined (16.6 mm SL), the parietal and nuchal spines are fused. Additional spines include a second posttemporal spine fused with the first, a fourth spine on the anterior preopercular spine row, and a supracleithral spine.

Head spines of Pacific larvae of *T. pingeli* were visible at an earlier stage of development than for Atlantic larvae. Spines were not visible in Atlantic *T. pingeli* until late flexion (>13 mm SL).

Morphological and other character comparisons. Among species occurring in the North Pacific Ocean and Bering Sea, larvae of *Triglops pingeli* are most similar to *T. forficatus*, but differ in most meristic counts: 45–51 (vs. 52–54) vertebrae, 23–26 (vs. 28–30) dorsal-fin rays, 21–27 (vs. 29–32) anal-fin rays, and 17–21 (vs. 20–22) pectoral-fin rays. In addition, larvae of *T. pingeli* can be differentiated from those of *T. forficatus* by having less pigment on the dorsal surface of the head, a concentration of very small external melanophores on the lateral and ventral surfaces of the gut near the anus (pigment finer than similar pigment on *T. forficatus*), little or no pigment on the ventral caudal finfold and base of the caudal-fin rays, the earlier appearance of head spines (late preflexion), and larger head spines throughout flexion and postflexion. Among species occurring in the North Atlantic Ocean, characters that distinguish larvae of *Triglops pingeli* from *T. murrayi* and *T. nybelini* include a generally higher number of PVMs at all stages of development (23–49, Table 3) and larger head spines through late flexion and postflexion.

Morphological comparisons of larvae of *Triglops pingeli* with all species resulted in significant differences for some measurements. Except for *T. murrayi*, preflexion *Triglops pingeli* had a significantly smaller eye diameter/HL, flexion *T. pingeli* had a significantly smaller eye diameter/HL, and postflexion *T. pingeli* had a significantly

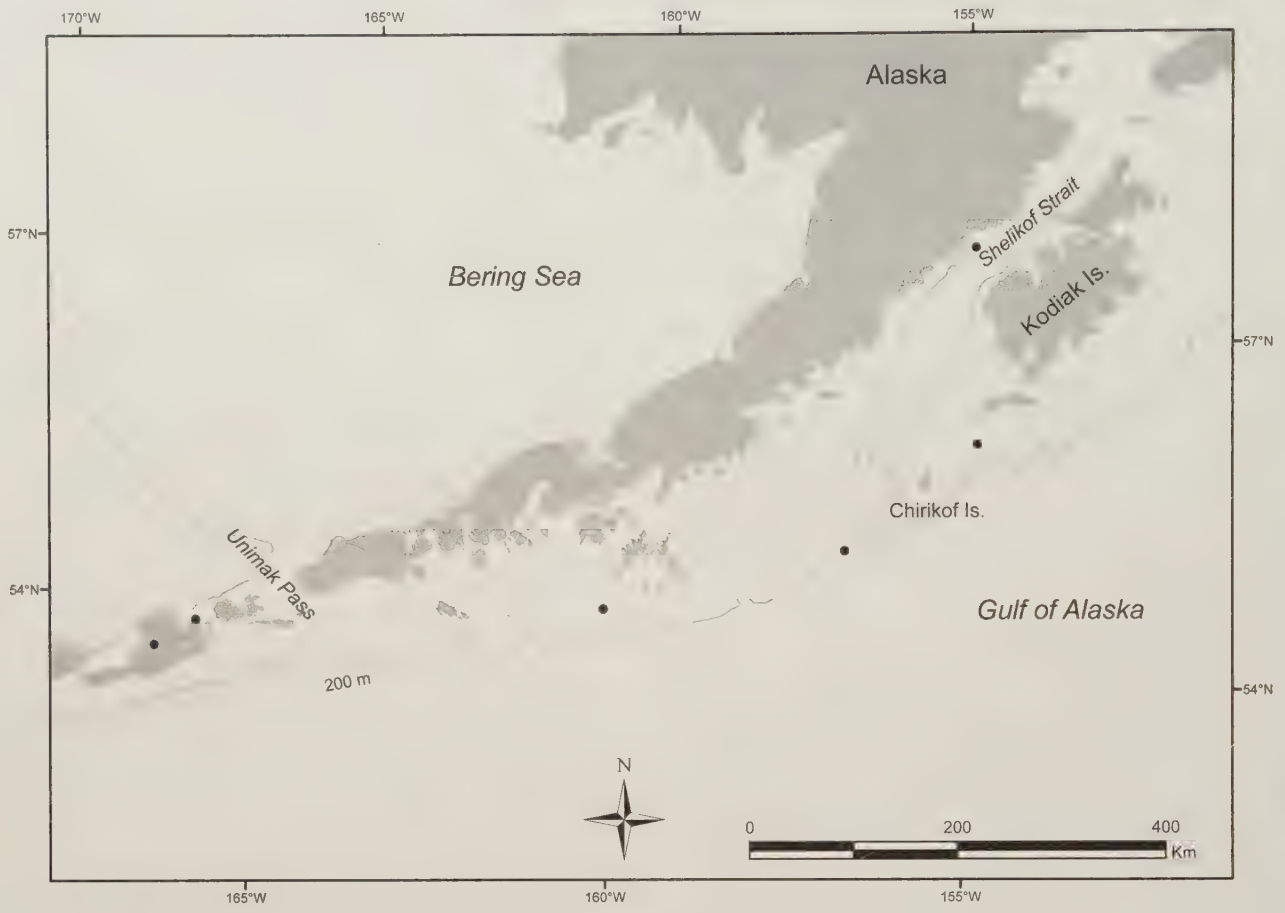

Figure 13

Distribution of material examined of larvae of *Triglops scepticus* in the Bering Sea and Gulf of Alaska. Each symbol may indicate more than one capture; bathymetry line equals 200 m.

smaller eye diameter/HL (because of small sample size in *T. murrayi*, head length/SL was not significant for the ANCOVA at 5%, but was close, so an ANOVA was run without head length/SL as a covariate) (Table 4).

Among the Pacific group of species, preflexion larvae of *Triglops pingeli* had a significantly smaller eye diameter/HL (Appendix 8), flexion *T. pingeli* had a significantly greater snout length/HL (Appendix 9) and significantly smaller eye diameter/HL (Appendix 10), and postflexion *T. pingeli* had a significantly smaller eye diameter/HL than other larvae (Appendix 11). Among the Atlantic group of species, flexion *T. pingeli* had a significantly greater pectoral-fin length/SL than *T. murrayi* and *T. nybelini* (Appendix 5).

Triglops scepticus, spectacled sculpin (Figs. 13–14)

Material examined. Eight specimens (9.0–19.0 mm SL) examined. Bering Sea: UW 125999, 1 (13.6 mm), 53°43.0′N, 166°53.0′W, 0–105 m depth, Tucker net, 04 June 1986; UW 105076, 3 (13.6–18.5 mm), 54°18.0′N, 166°21.0′W, 0–81 m depth, Tucker net, 02 June 1986. Gulf of Alaska: UW 059622, 1 (9.0 mm), 56°10.0′N, 154°50.0′W, 0–60 m depth, bongo net, 22 May 1982; UW 050998, 1 (9.3 mm), 57°51.7′N, 154°53.7′W, 0–276 m depth, bongo net, 07 April 1986; UW 126000, 1 (16.7 mm), 55°13.1′N, 156°49.2′W, 0–99 m depth, bongo net, 26 May 1996; UW 126001, 1 (19.0 mm), 54°34.6′N, 160°23.1′W, 0–101 m depth, bongo net, 24 May 2005.

Occurrence. Adults of *Triglops scepticus* are restricted to waters in and adjacent to the North Pacific Ocean and Bering Sea. Adults are found from the southern Sea of Japan and Tatarskiy Strait to Navarin Canyon in the western Bering Sea, outer shelf and slope regions of the eastern Bering Sea, throughout the Commander and Aleutian Islands, east to Kodiak Island in the Gulf of Alaska, and southward to southeast Alaska (Pietsch, 1993; Mecklenburg et al., 2002).

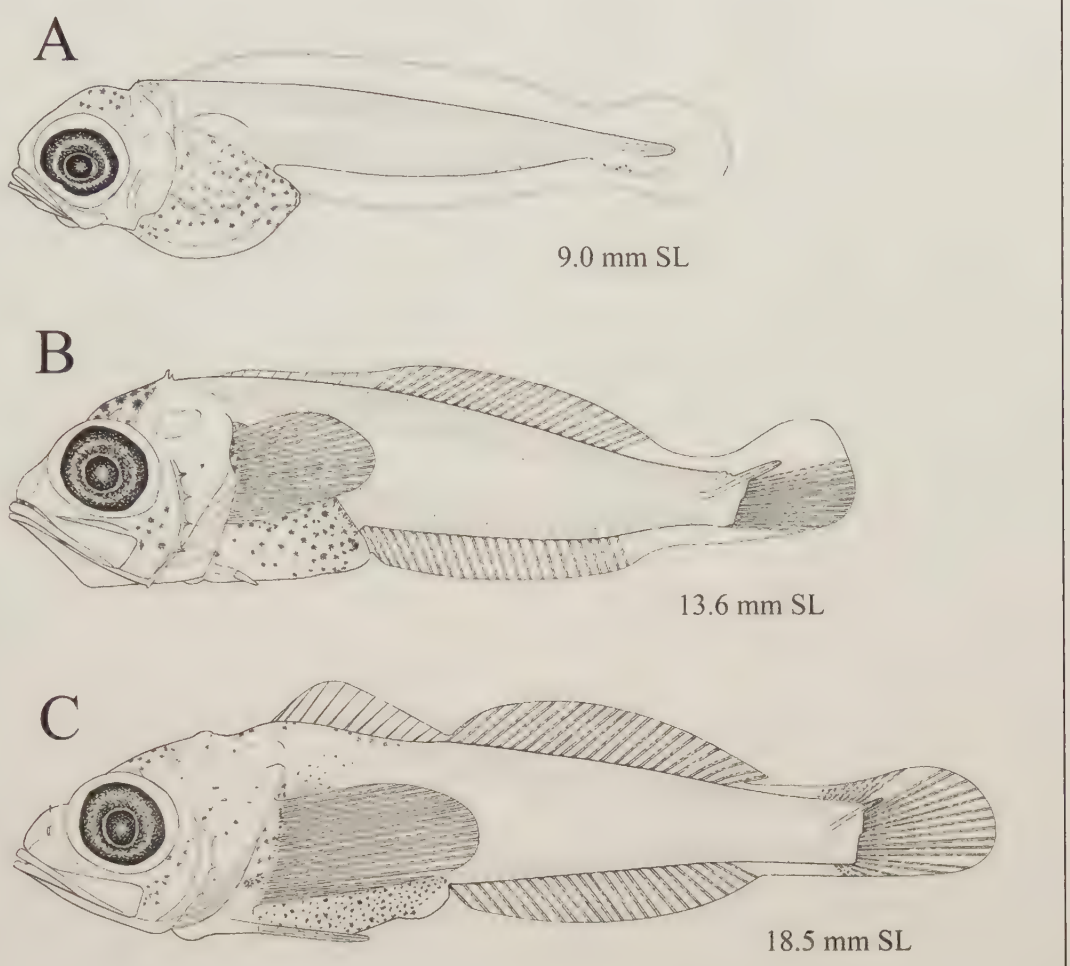

Figure 14

Larvae of *Triglops scepticus*: (A) preflexion, 9.0 mm SL (standard length), UW 059622; (B) flexion, 13.6 mm SL, UW 105076; (C) postflexion, 18.5 mm SL, UW 105076. Illustrations by B. Vinter.

Larvae of *Triglops scepticus* have been collected just west of Unimak Pass, along the outer shelf east and west of Chirikof Island, and in Shelikof Strait (Fig. 13). Larvae are collected from April to June.

Pigment. Only eight larvae were available for examination to describe changes in pigmentation during development. Larvae of *Triglops scepticus* have moderate pigment on the head and moderate to heavy pigment on the gut. In most specimens, postanal pigment is restricted to fewer than five PVM and fewer than ten internal melanophores located just above the ventral midline. The PVM are initially external, become embedded with development, and are not visible by postflexion.

Head pigment in preflexion larvae consists primarily of dorsal pigment on the forebrain, midbrain, hindbrain, and nape; some pigment is visible on the dorsal rim of the orbit. Internal pigment can be seen on the side of the midbrain and nape. Several melanophores are present on the pectoral-fin base. Pigment on the gut is initially moderate and restricted to the dorsal and lateral surfaces and surrounding the anus. Pigment on the dorsal and lateral surface of the gut becomes heavy and ventral pigment develops later in preflexion larvae posterior to the isthmus and on the posterior third of the gut. Postanal pigment begins as two PVM at 75% SL (Fig. 14A). A short series (~10) of internal melanophores just above the ventral midline starting at about 60% SL is visible, in addition to a third melanophore immediately posterior to the other PVM on the larger preflexion larva. Five to six melanophores are present on the ventral caudal-fin anlage.

Head pigment increases in flexion larvae. Internal melanophores on the forebrain and dorsal midbrain

and both internal and external pigment are present on the nape. Pigment is visible on the membrane between the upper jaw and snout. Diffuse pigment develops in the posttemporal area, in the preopercular area, and in the opercular area even with the midline of the eye (Fig. 14B). More pigment develops on the pectoral-fin base. The gut is completely pigmented except for the anterior one-half to two-thirds of its ventral surface and the anus; pigment on the dorsal surface is heavier than on the rest of the gut. Postanal body pigment may be difficult to see in some flexion larvae. In addition to two internal PVM at 75% SL, melanophores may be present on the hypaxial myomeres near the developing caudal fin, on the ventral finfold of the caudal peduncle, and on the upper and lower developing caudal-fin rays.

Pigment continues to increase on the head of postflexion larvae. More internal pigment is present on the midbrain, more external pigment is present in the preopercular and opercular areas, and pigment is visible near the nares. Pigment appears on the lower jaw and outlines the edge of the preopercle anterior to the spines. A light speckling of pigment appears on the nape, near the base of the dorsal spines, and on the lateral body over the gut (Fig. 14C). Pigment increases from moderate to heavy on the pectoral-fin base. In addition to a few pigment spots in the center of the isthmus, the anterior edge of the isthmus is lined with moderately-spaced melanophores. A few melanophores are at the base of the pelvic fins. Pigment on the gut is heavy, covering all areas except for the anus, and the dorsal surface of the gut appears black; individual melanophores are visible under the surface of the skin. While most gut pigment is internal, small external melanophores are present on the lateral and ventral surface of the gut. No pigment is visible on the postanal body in postflexion larvae.

Proportions. Notochord flexion in *Triglops scepticus* begins after 9 mm SL and is complete by 18.5 mm SL. For those larvae examined, most body measurements for *T. scepticus* increase from preflexion to flexion stage and then decrease minimally during postflexion (Table 2). These are snout to anus length/SL, snout to first dorsal-fin length/SL, body depth/SL, head length/SL, and snout length/HL. Eye diameter/HL decreases throughout development. Interorbital width/HL increases in postflexion larvae only. Pectoral-fin length/SL increases from preflexion to postflexion.

Spination. Ossification of spines could not be determined due to the insufficient number of specimens for clearing and staining. A single parietal spine is present in preflexion larvae. By flexion stage, single parietal, nuchal, and postocular spines and a single row of four preopercular spines are present. Nasal spines are present in postflexion larvae and the parietal and nuchal spines are overgrown with skin.

Morphological and other character comparisons. Larvae of *Triglops scepticus* have a low vertebral count (45–46), a low dorsal-fin ray count (21–24), and the fewest numbers of PVM, which begin farther away from the anus than any other species of *Triglops* that have a PVM series (Table 3).

In comparison with all other species of *Triglops*, preflexion larvae of *T. scepticus* have a significantly larger eye diameter/HL than all other larvae except *T. nybelini* (Table 4). Flexion larvae of *T. scepticus* have a significantly greater snout to anus length/SL (Appendix 1), greater eye diameter/HL (Appendix 12), greater body depth/SL (Appendix 13), and greater interorbital width/HL (Appendix 14) than all other larvae. Postflexion larvae of *T. scepticus* have a significantly greater snout to anus length/SL than all larvae except *T. murrayi* (Table 4) and a significantly greater body depth/SL than all larvae except *T. macellus* (Table 4).

In comparison with larvae in the Pacific group of species, preflexion larvae of *Triglops scepticus* have a significantly larger eye diameter/HL than all other larvae (Appendix 8). Flexion larvae of *T. scepticus* have a significantly greater snout to anus length/SL (Appendix 1), greater body depth/SL (Appendix 3), and larger eye diameter/HL (Appendix 10) than all other larvae. Postflexion larvae of *T. scepticus* have a significantly greater snout to anus length/SL than all other larvae (Appendix 15).

Discussion

Identification of most larval *Triglops* was not possible prior to Pietsch's (1993) revision of the genus; adult meristic counts were either lacking or overlapping, thus preventing differentiation of most species at all stages. Revised meristics enabled identification of most late flexion and postflexion larvae; for *T. forficatus*, the high vertebral count permitted positive identification at all stages. Pigment patterns of larvae with full meristic counts were used to identify younger larvae. This process allowed identification of most of our specimens of *Triglops* collected in the North Pacific Ocean and Bering Sea (poor condition of a small number of larvae prevented identification to species). Although larvae of *Triglops scepticus* were identifiable on the basis of pigment pattern and body morphology, there were few specimens available for examination. Existing morphological data and pigment characters may change as more specimens are collected. Of larvae reported in the literature, *Triglops* A as presented by Matarese

et al. (1989) is probably *T. pingeli*; the meristic counts (as illustrated: 46–47 myomeres, 22 anal-fin rays, 17 pectoral-fin rays), large head spines, and presence of two postocular spines on the 16.9-mm larva are non-overlapping characters for this species. *Triglops* sp. described by Richardson and Washington (1980) is probably *T. macellus*, as surmised by the authors. The myomere count is low (47), but the pectoral fin count (16) is too low for any other co-occurring species. Also, the pattern of heavy pigment on the gut and absence of pigment on the postanal body is exclusive to *T. macellus*. Larvae illustrated by Blackburn (1973) appear to resemble the larvae described by Richardson and Washington (1980); however, median and caudal-fin rays are shown as forming on the 8.3-mm larva and none of the larvae described herein begin fin-ray development at that size. Also, the ventral gut area is unpigmented on the 12-mm larva; the entire gut of our *T. macellus* larvae is pigmented at that size. Identification of these larvae may not be possible without myomere counts.

Identification of the three species co-occurring in the western North Atlantic Ocean is difficult because of the large degree of overlap of many meristic characters. The description of *Triglops murrayi* larvae presented here differs from published identifications, but is most similar to that of Khan (1972). Some of our larvae developed dorsolateral and ventrolateral postanal pigment at about 10 mm SL that was not described by Khan (1972). Pavlov et al. (1992) described dorsolateral pigment on 12.0 and 14.2-mm larvae. They also described dorsal midline pigment on 14.2 and 20.2-mm larvae, which was not reported by Khan (1972) or Fahay (1983, 2007). The dorsolateral and dorsal midline pigment illustrated on the larvae in Pavlov et al. (1992) is found in *T. nybelini*; however, the dorsal-fin-ray count for the 20.2-mm larva (22) is specific for *T. murrayi*. Light speckled pigment along the dorsal midline was present only on our largest postflexion larva (23.4 mm SL) and may be the beginning of juvenile pigment. Fahay (2007) described flexion in *T. murrayi* occurring at 12 mm or larger; however, flexion was evident in our larvae as early as 10.5 mm SL.

The single published description of *Triglops nybelini* (27 mm SL; Dunbar and Hildebrand, 1952) lists the pectoral-fin-ray count of 22 and large eye as diagnostic characters of the species, and in addition describes the dark line of pigment extending along the dorsal midline from the front of the first dorsal fin to the caudal fin. Dorsal midline pigment first appears during early flexion in our larvae of *T. nybelini* along the base of the developing dorsal-fin rays. Dorsal notochord pigment, which is unique to this species, appears in late preflexion and persists through midflexion. As with *Triglops scepticus*, there were few specimens of *T. nybelini* available for examination. Morphology data and pigment characters may change as more specimens are collected.

Published identifications of larvae of *Triglops pingeli* are incomplete, and several are based on misidentified specimens. Rass (1949) illustrated a 10-mm larva from the Barents Sea with dorsal midline pigment, a very large eye (50% HL), and a protruding lower jaw; this last character was described by Pietsch (1993) as peculiar to adult *T. nybelini* among species of *Triglops* found in that area. The eye diameter of *T. pingeli* is smaller than the eyes of all other *Triglops* larvae at all stages of development (Appendices 10, 12–13) and adults have smaller eyes than most *Triglops* (Pietsch, 1993). Therefore, the larvae in Rass (1949) is most likely *T. nybelini*. Koefoed (1907) described eight larvae as *T. pingeli*; however, the five largest larvae (18.5–22.0 mm) have dorsal-fin-ray counts of 22, which indicates they could only be *T. murrayi*. The dorsal (25) and anal-fin-ray count (25) for the 16.5-mm larva of Koedfoed (1907; Fig. 5) could identify this larva as either *T. pingeli* or *T. nybelini*. The illustration shows dorsal midline and lateral line pigment, which was apparent on none of our *T. pingeli* specimens, and is more like pigment belonging to larvae of *T. nybelini* rather than those of *T. pingeli*.

The genus *Triglops* is morphologically distinct from other cottids, but there is no consensus as to its relationship to other members of the family. Larval morphology of *Triglops* was examined by Richardson (1981) who placed the genus in a phenetic group of five genera that share body shape (pointed snout, slender body), pigment characters (heavy pigment on dorsal surface of the gut and a PVM series), and the presence of four preopercular spines. In an unpublished study based on osteological characters by Washington and Richardson (Washington et al., 1984), an additional eight genera were added to Richardson's (1981) group on the basis of the presence of a distinct preopercular bony shelf and other head spines. Although this group (the *Myoxocephalus* group) is the least well-defined of the cottid groupings, the external morphological characters used by Richardson (1981) corresponded well with osteological characters used in the later study. However, no close affinities between *Triglops* and other genera within this group could be ascertained.

Yabe (1985) examined morphological characters of adults and proposed *Triglops* to be a sister group of a "*Radulinus*-group" that included *Radulinus*, *Asemichthys*, and *Astrocottus*. Smith and Wheeler (2004) reanalyzed Yabe's (1985) work and found *Triglops* to have close ties to no other cottid genera, which was the same outcome to their own genetic analysis. Further analysis combining morphological data, ontogenetic characters, and expanded molecular data, as suggested by Smith and Wheeler (2004), may clarify the position of the genus *Triglops* within the family Cottidae.

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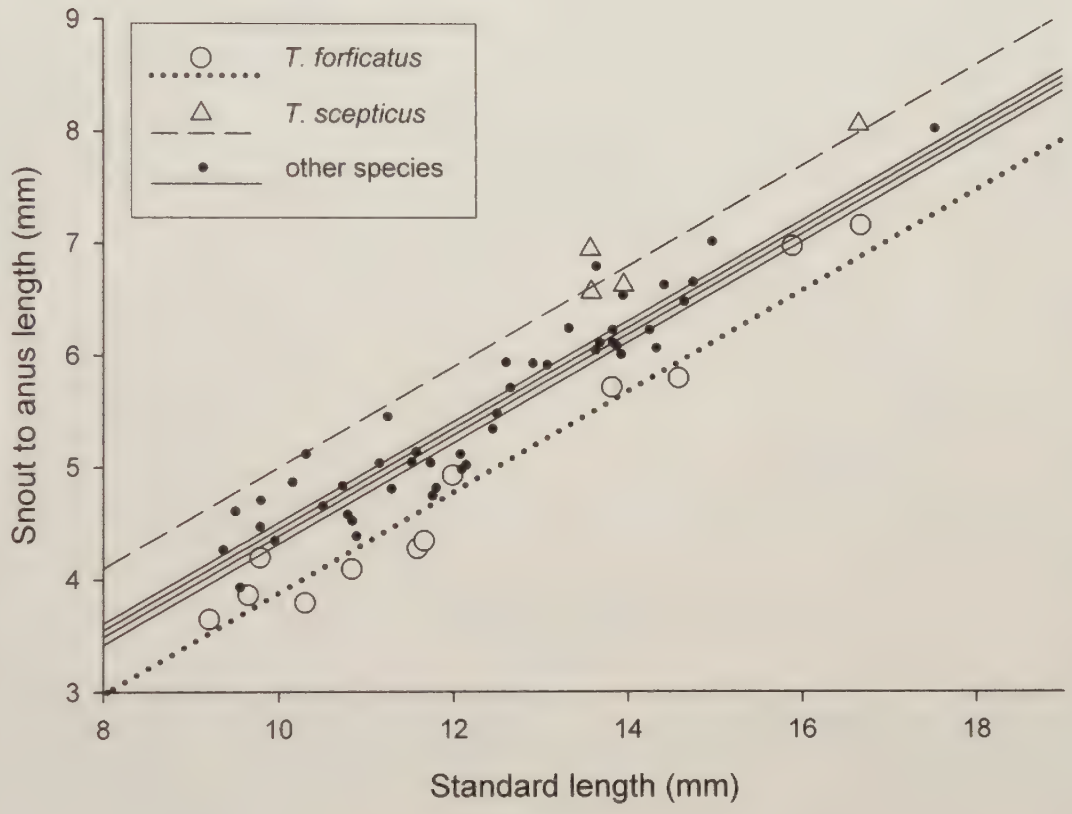
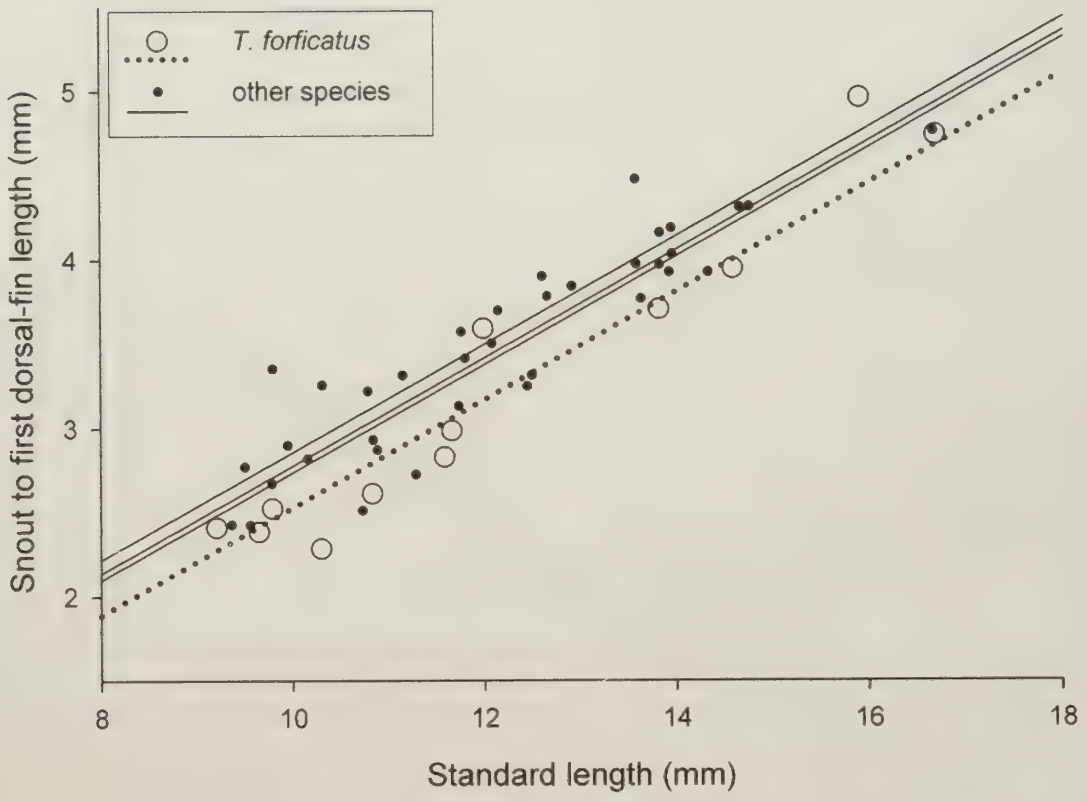
Appendices



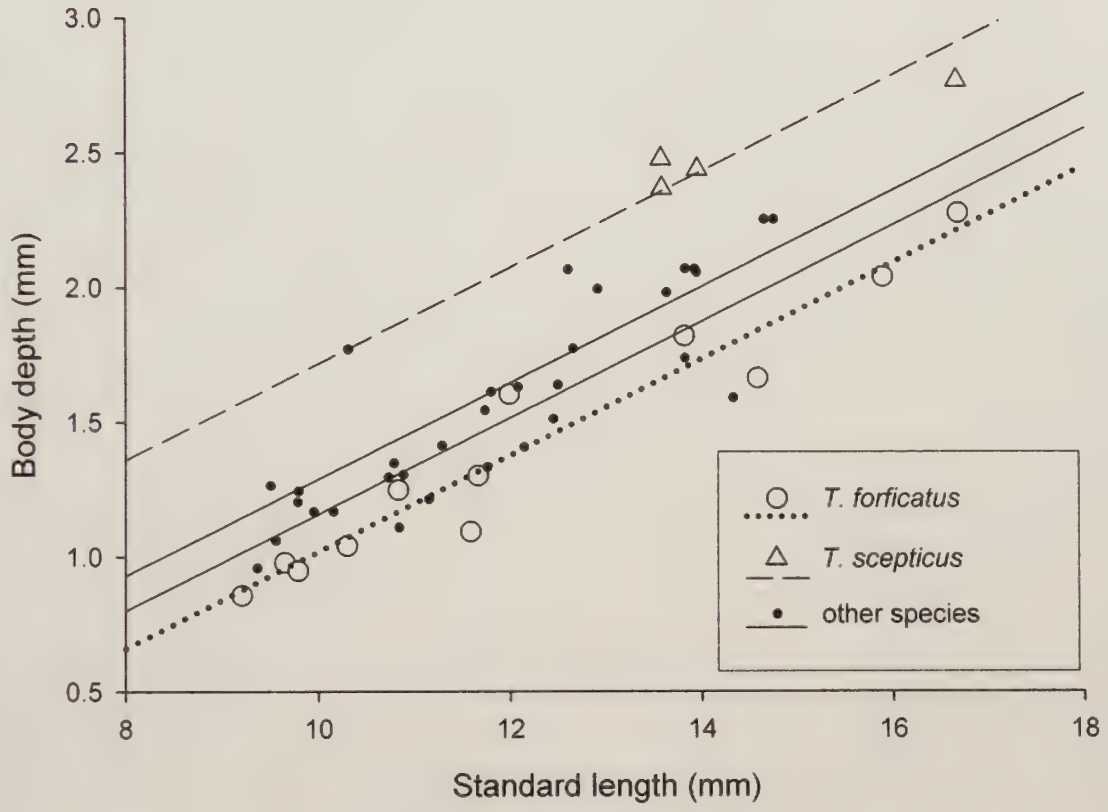
Appendix 1

Comparison of morphometric measurements of flexion larvae of *Triglops*, snout to anus length vs. standard length. Other species represented by solid lines and black dots are *T. macellus*, *T. murrayi*, *T. pingeli*, and *T. nybelini*. Symbols represent measured values for each species; lines represent equations generated by analysis of covariance ($P<0.05$).



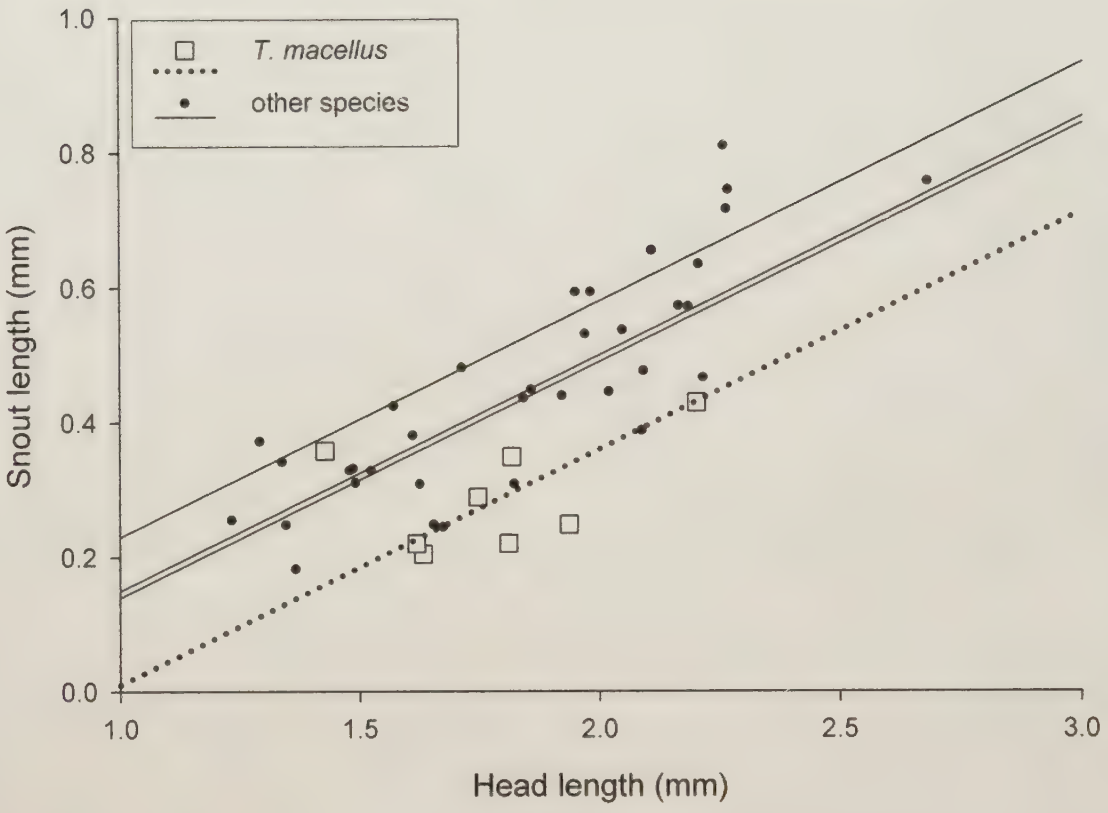
Appendix 2

Comparison of morphometric measurements of flexion larvae of Pacific species of *Triglops* (*T. forficatus*, *T. macellus*, *T. pingeli*, and *T. scepticus*), snout to first dorsal-fin length vs. standard length. Other species represented by solid lines and black dots are *T. macellus*, *T. pingeli*, and *T. scepticus*. Symbols represent measured values for each species; lines represent equations generated by analysis of covariance ($P<0.05$).



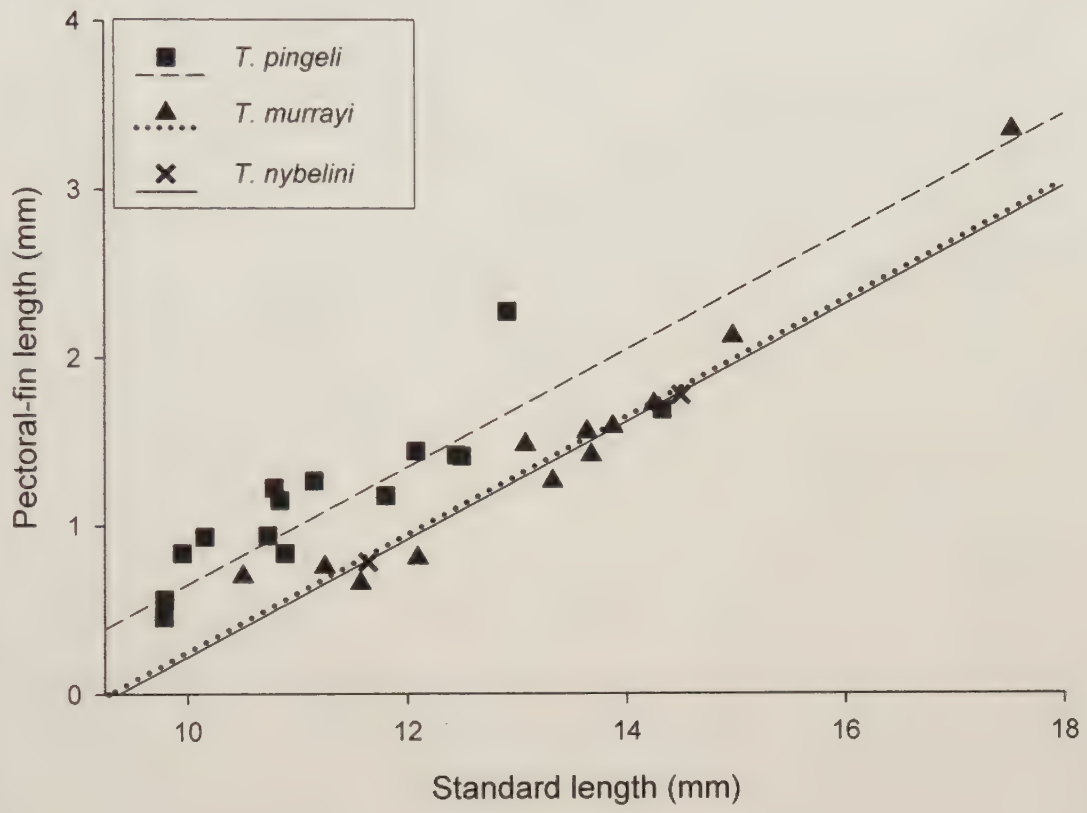
Appendix 3

Comparison of morphometric measurements of flexion larvae of Pacific species of *Triglops* (*T. forficatus*, *T. macellus*, *T. pingeli*, and *T. scepticus*), body depth vs. standard length. Other species represented by solid lines and black dots are *T. macellus* and *T. pingeli*. Symbols represent measured values for each species; lines represent equations generated by analysis of covariance ($P<0.05$).



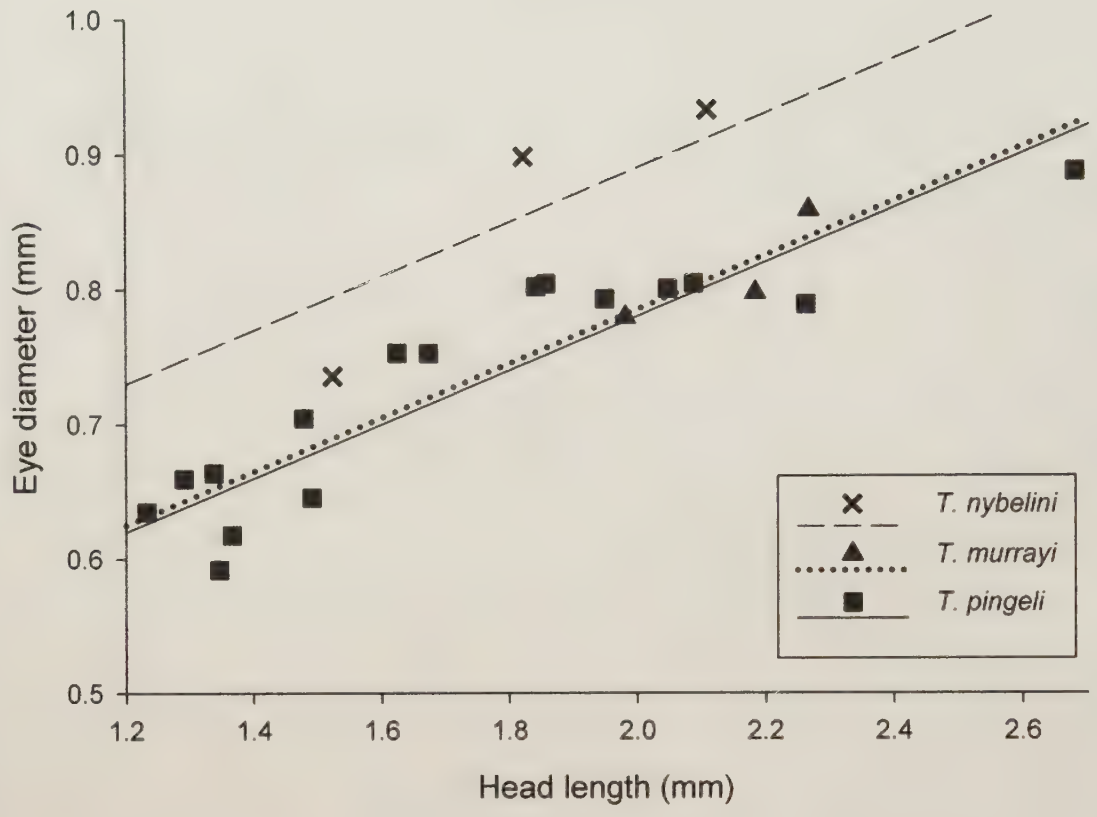
Appendix 4

Comparison of morphometric measurements of preflexion larvae of *Triglops*, snout length vs. head length. Other species represented by solid lines and black dots are *T. forficatus, T. murrayi, T. pingeli, T. nybelini,* and *T. scepticus.* Symbols represent measured values for each species; lines represent equations generated by analysis of covariance (P=0.10).



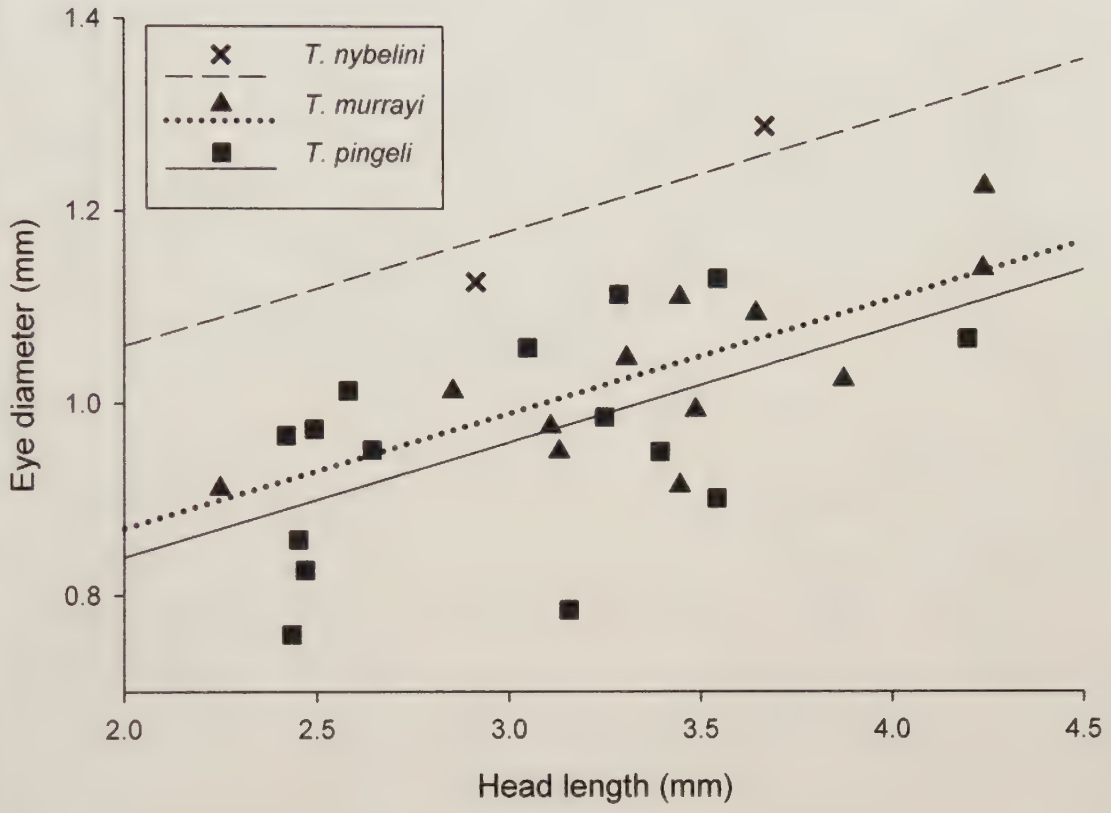
Appendix 5

Comparison of morphometric measurements of flexion larvae of Atlantic species of *Triglops* (*T. murrayi, T. nybelini*, and *T. pingeli*), pectoral-fin length vs. standard length. Symbols represent measured values for each species; lines represent equations generated by analysis of covariance ($P<0.05$).



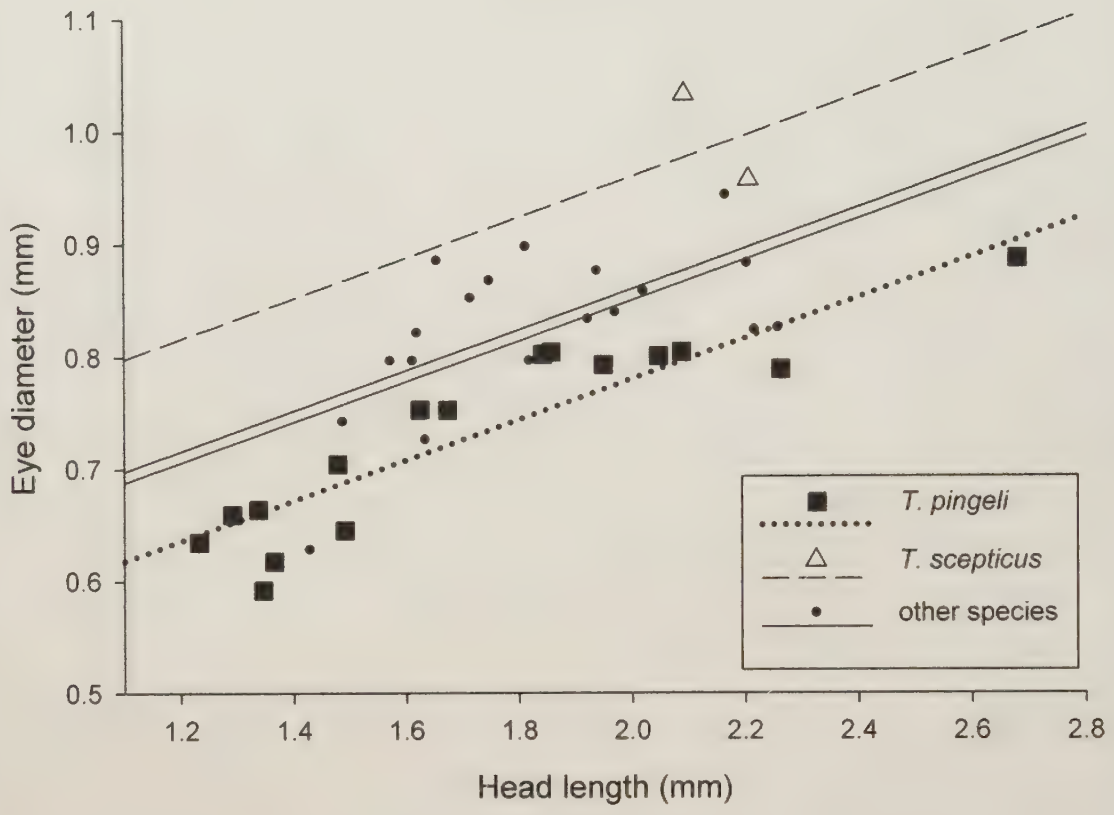
Appendix 6

Comparison of morphometric measurements of preflexion larvae of Atlantic species of *Triglops* (*T. murrayi*, *T. nybelini*, and *T. pingeli*), eye diameter vs. head length. Symbols represent measured values for each species; lines represent equations generated by analysis of covariance ($P<0.05$).



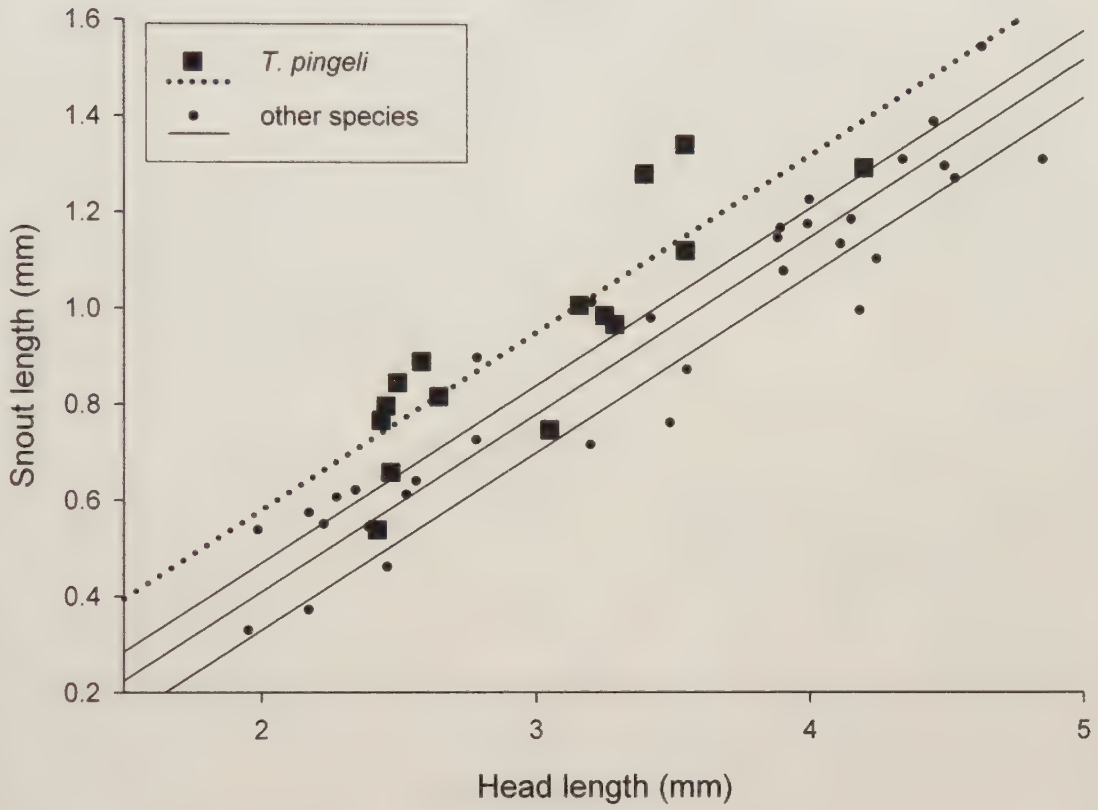
Appendix 7

Comparison of morphometric measurements of flexion larvae of Atlantic species of *Triglops* (*T. murrayi*, *T. nybelini*, and *T. pingeli*), eye diameter vs. head length. Symbols represent measured values for each species; lines represent equations generated by analysis of covariance ($P<0.05$).



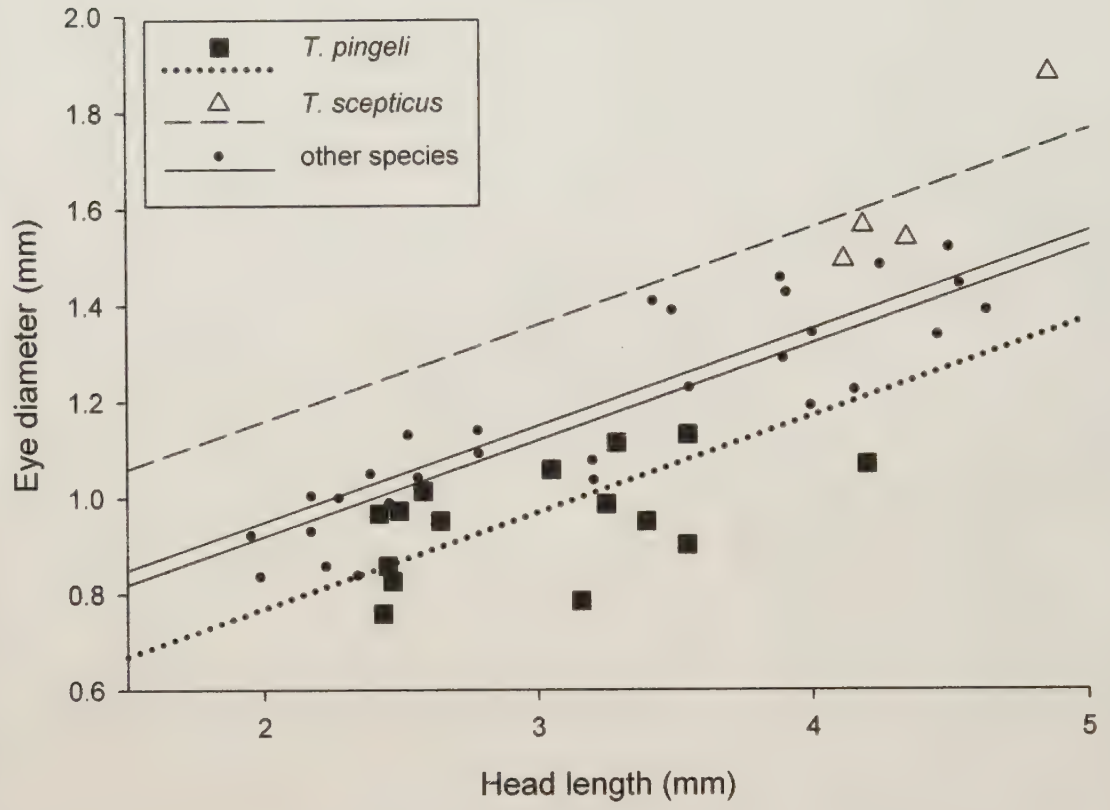
Appendix 8

Comparison of morphometric measurements of preflexion larvae of Pacific species of *Triglops* (*T. forficatus, T. macellus, T. pingeli,* and *T. scepticus*), eye diameter vs. head length. Other species represented by solid lines and black dots are *T. forficatus* and *T. macellus.* Symbols represent measured values for each species; lines represent equations generated by analysis of covariance ($P<0.05$).



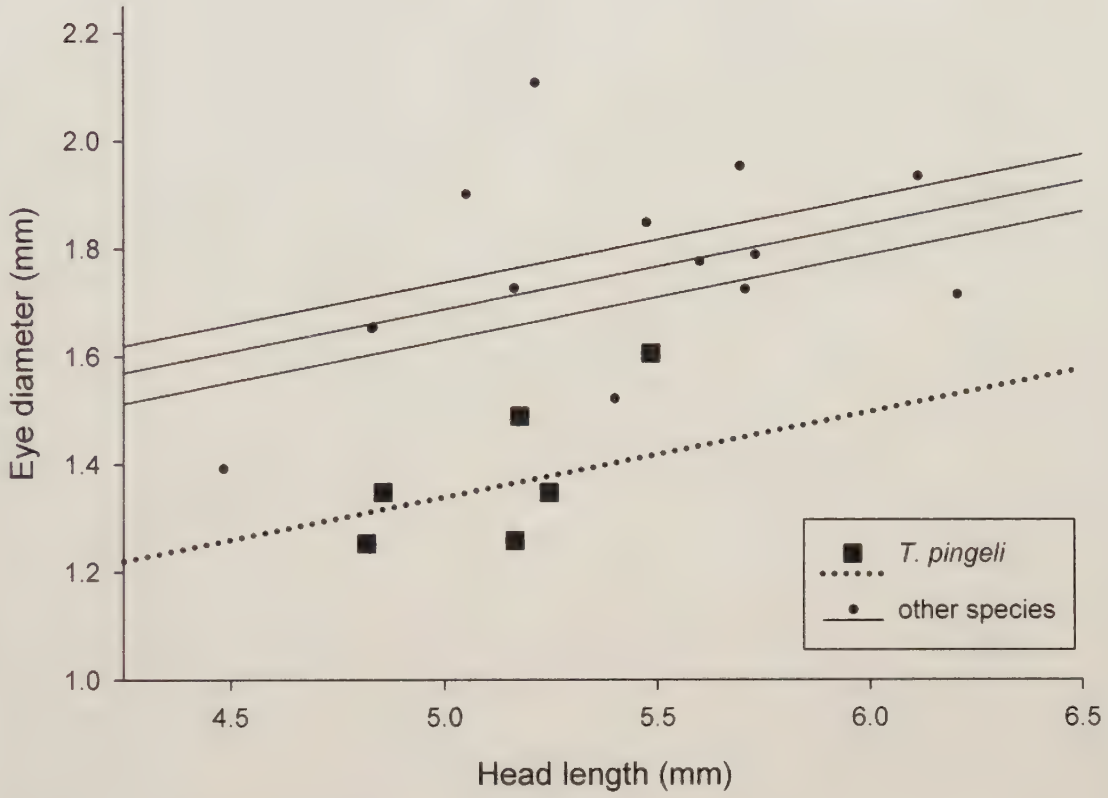
Appendix 9

Comparison of morphometric measurements of flexion larvae of Pacific species of *Triglops* (*T. forficatus, T. macellus, T. pingeli,* and *T. scepticus*), snout length vs. head length. Other species represented by solid lines and black dots are *T. forficatus, T. macellus,* and *T. scepticus.* Symbols represent measured values for each species; lines represent equations generated by analysis of covariance ($P<0.05$).



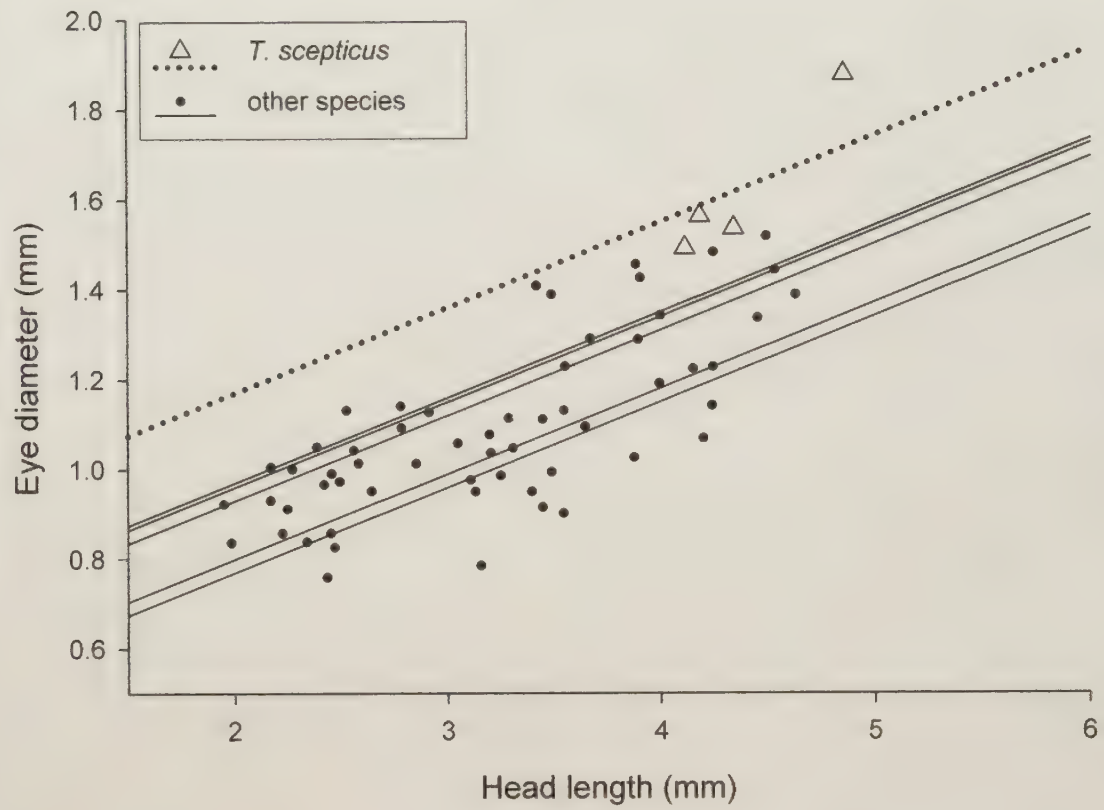
Appendix 10

Comparison of morphometric measurements of flexion larvae of Pacific species of *Triglops* (*T. forficatus*, *T. macellus*, *T. pingeli*, and *T. scepticus*), eye diameter vs. head length. Other species represented by solid lines and black dots are *T. forficatus* and *T. macellus*. Symbols represent measured values for each species; lines represent equations generated by analysis of covariance ($P<0.05$).



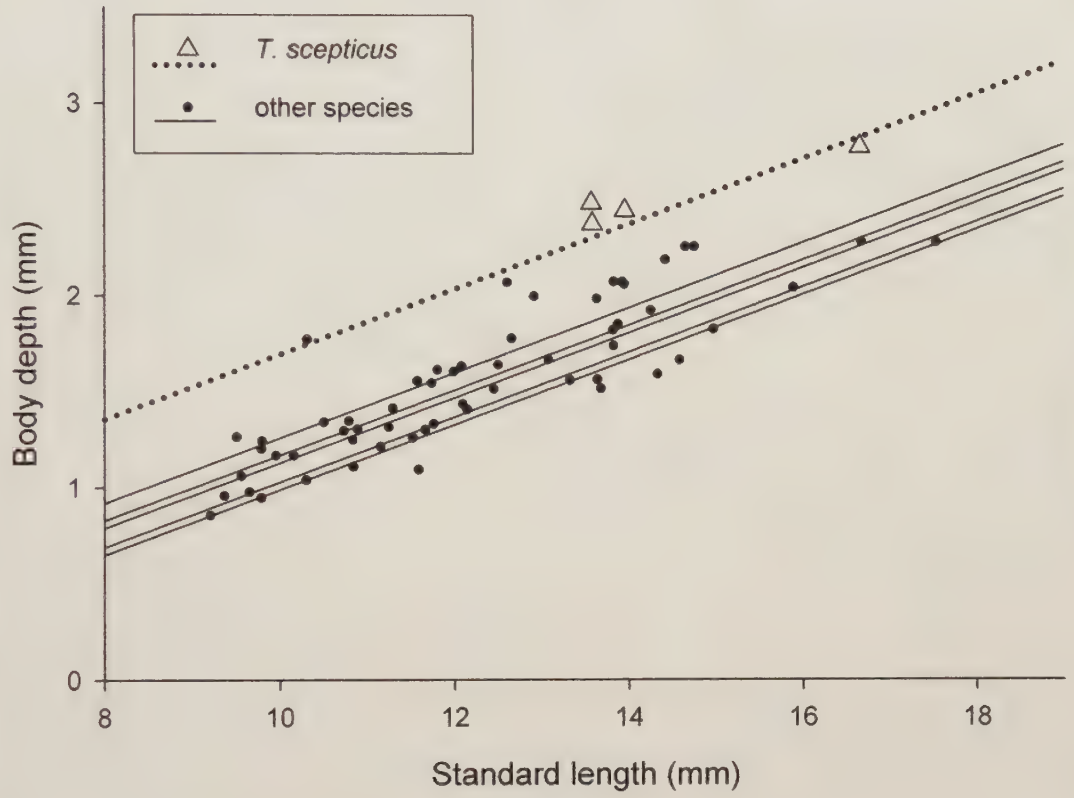
Appendix 11

Comparison of morphometric measurements of postflexion larvae of Pacific species of *Triglops* (*T. forficatus, T. macellus, T. pingeli,* and *T. scepticus*), eye diameter vs. head length. Other species represented by solid lines and black dots are *T. forficatus, T. macellus,* and *T. scepticus.* Symbols represent measured values for each species; lines represent equations generated by analysis of covariance ($P<0.05$).



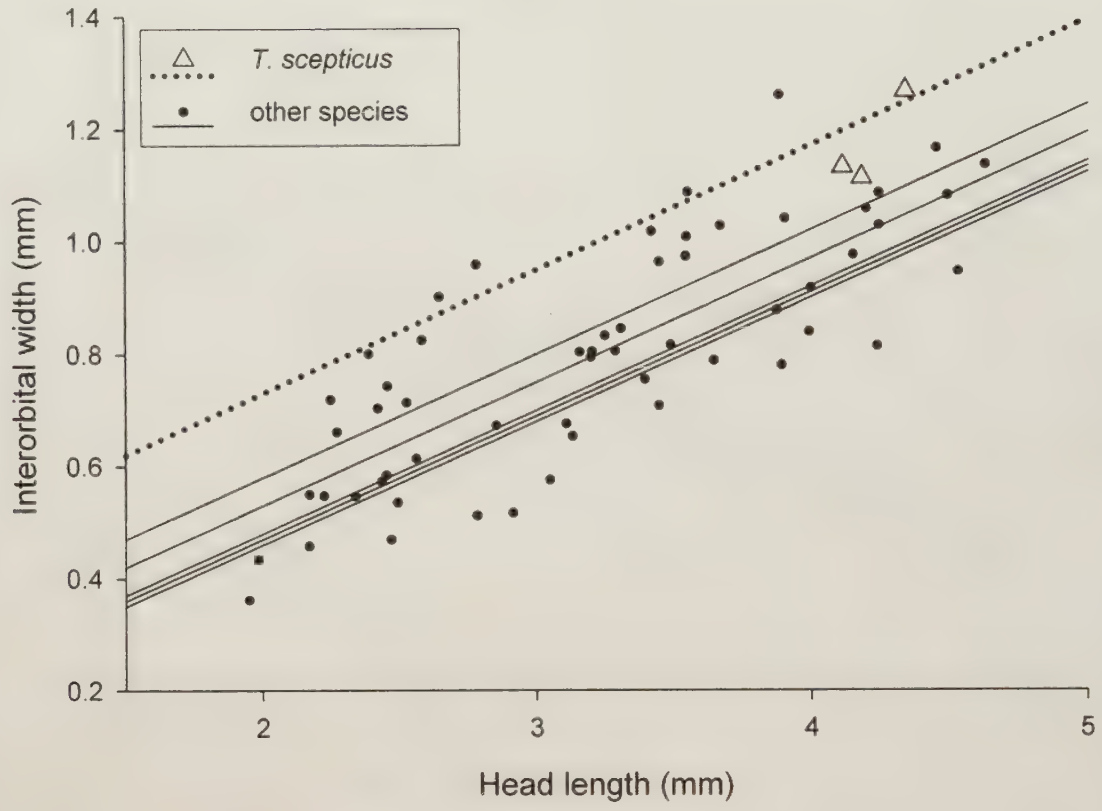
Appendix 12

Comparison of morphometric measurements of flexion larvae of *Triglops*, eye diameter vs. head length. Other species represented by solid lines and black dots are *T. forficatus, T. macellus, T. murrayi, T. nybelini,* and *T. pingeli.* Symbols represent measured values for each species; lines represent equations generated by analysis of covariance ($P<0.05$).



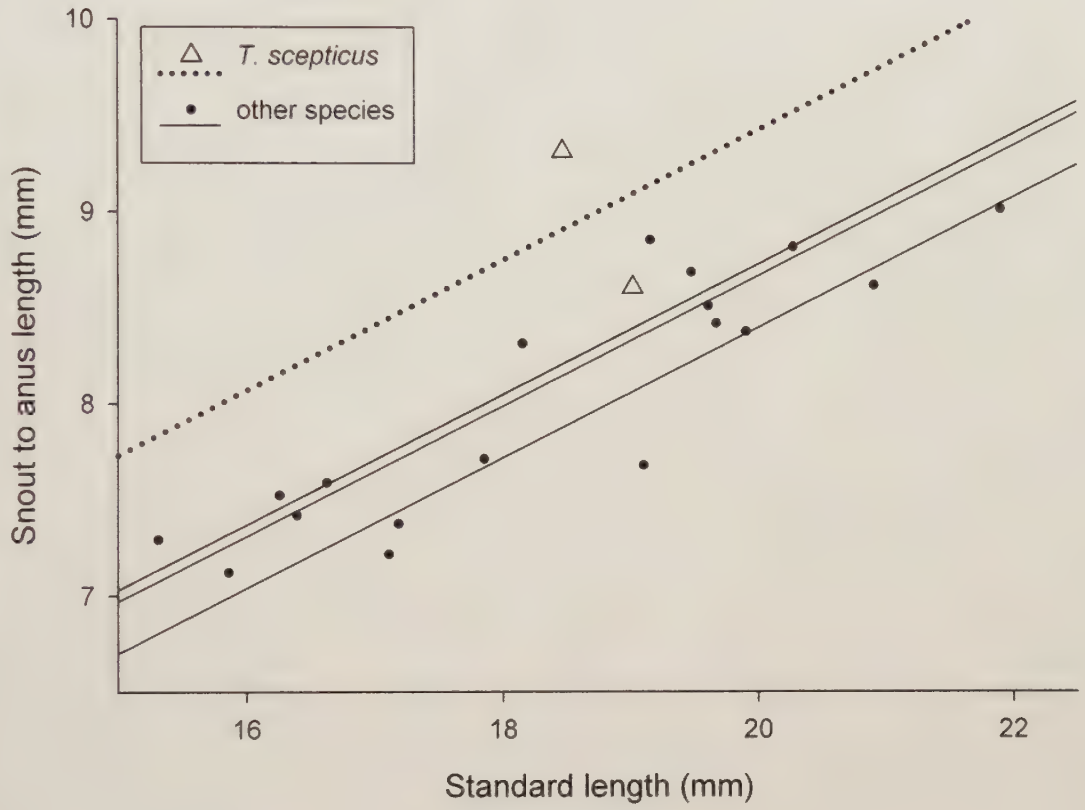
Appendix 13

Comparison of morphometric measurements of flexion larvae of *Triglops*, body depth vs. standard length. Other species represented by solid lines and black dots are *T. forficatus, T. macellus, T. murrayi, T. nybelini,* and *T. pingeli.* Symbols represent measured values for each species; lines represent equations generated by analysis of covariance ($P<0.05$).



Appendix 14

Comparison of morphometric measurements of flexion larvae of *Triglops*, interorbital width vs. head length. Other species represented by solid lines and black dots are *T. forficatus, T. macellus, T. murrayi, T. nybelini,* and *T. pingeli.* Symbols represent measured values for each species; lines represent equations generated by analysis of covariance ($P<0.05$).



Appendix 15

Comparison of morphometric measurements of postflexion larvae of Pacific species of *Triglops* (*T. forficatus, T. macellus, T. pingeli,* and *T. scepticus*), snout to anus length vs. standard length. Other species represented by solid lines and black dots are *T. forficatus, T. macellus,* and *T. pingeli.* Symbols represent measured values for each species; lines represent equations generated by analysis of covariance ($P<0.05$).

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